THE INFLUENCE OF SPECIES DIVERSITY ON ECOSYSTEM PRODUCTIVITY IN DIFFERENT ENVIRONMENTS: EXPERIMENTAL PLANT COMMUNITIES AND THEORY

By

Jason D. Fridley

A dissertation submitted to the faculty of the University of North Carolina at Chapel Hill in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Biology.

Chapel Hill

2002

Approved by:

Advisor: Professor Robert K. Peet

Reader: Professor Peter S. White

Reader: Professor Alan E. Stiven

Reader: Professor James S. Clark

Reader: Professor Michael A. Huston

© 2002
Jason D. Fridley
ALL RIGHTS RESERVED

ABSTRACT

Jason D. Fridley:

The influence of species diversity on ecosystem productivity in different environments: experimental plant communities and theory

(Under the direction of Robert K. Peet)

The relationship between species diversity and the functioning of ecosystems is one of the most critical but contentious issues in contemporary ecology, and plant ecologists are strongly divided over whether ecosystems of greater plant diversity exhibit higher rates of biomass production. Experimental evidence that plant species diversity has positive effects on production appears to conflict with correlations of species diversity and standing biomass in natural communities. This may be due to the confounding effects of environmental factors, such as resource availability, that exert strong control over both diversity and productivity in natural systems. Unfortunately, the extent to which environmental conditions influence the diversity-productivity relationship is unknown; it is, therefore, difficult to establish the particular ecosystems in which species loss most affects ecosystem functioning.

I performed two field experiments using microcosm plant communities to explore whether the influence of plant species diversity on ecosystem productivity varies with environment. In the first experiment I constructed communities of differing species diversity and composition along a soil fertility gradient. Although the effects of fertility on production were far greater than that of diversity, diversity effects became more

pronounced as fertility increased. In a second experiment where similar communities with different levels of diversity were grown in different nutrient and light environments, the diversity-fertility interaction in the control of production was determined to be the result of light partitioning by species of different growth habits. These results suggest that, although diversity effects on production should generally be small compared to those associated with environmental factors, small-scale plant diversity may enhance productivity under certain environmental conditions.

I extended these experimental results by exploring three species interaction models within the context of the diversity-productivity relationship. As a whole, these theoretical models support observations that diversity effects increase with the resource availability, but by means that depend on whether species coexist by resource partitioning or processes resulting from non-equilibrium dynamics. Resource partitioning begets complementary resource use, where many species are needed to maximize resource harvesting. Coexistence by density-independent perturbations begets diversity effects that are related to dominance by species with particular resource-use traits.

ACKNOWLEDGEMENTS

I am very grateful to the many professors, colleagues, staff, and field assistants who have helped me bring this project to fruition. I have benefited tremendously from watching great ecologists at work, and many have provided me with extraordinary insight into my own dissertation work, including Jim Clark, Phil Grime, Michael Huston, Rob Jackson, Bob Peet, Alan Stiven, Peter White, and Kerry Woods. Michael Huston in particular was a constant source of constructive criticism and experimental ideas. He and Jim Clark, Alan Stiven, and Peter White deserve special thanks for guiding my dissertation work as four-fifths of my graduate committee. I am grateful to Jim Clark for allowing me frequent access to his lab group at Duke. Finally, I feel privileged to have developed as an ecologist under the wing of Bob Peet, my graduate advisor and mentor, who was never short on advice and support but gave me the freedom to work independently on my own ideas.

My lab colleagues were a constant source of inspiration, encouragement, conviviality, you name it—and of course the occasional hack (at hundreds of gas stations, on the top of several peaks, even deep within the bowels of Carlsbad Caverns). In particular, I learned a great deal about ecology from Becky Brown, my collaborator, critic, and frequent sparring partner, who provided me constant feedback and encouragement on all aspects of this dissertation. I am also grateful to Carol Ann McCormick for much helpful practical advice. Librarians Jeffery Beam and Bill Burke

made a researcher's job easy, and made the Botany Library at UNC one of my favorite places in the world.

My experimental work at Mason Farm Biological Preserve depended upon the support, advice, and physical help of many people. Johnny Randall and Alan Johnson at the North Carolina Botanical Garden and Mike Sears and Cliff Parks of the Biology Department were especially helpful in the design and coordination of my experimental setup. Planting and harvesting would have been impossible without field help volunteers, including Rob MacDonald, Michael Lee, Becky Brown, John Boetsch, Beth Fetrow, Dale Fridley, Eric Fridley, Genevieve Fridley, Jeff Hughey, Mary James, Len Krall, Adel Peterdi, Leah Saturen, Alaa Wally, Ken Wurdack, and Weimin Xi. Tim Allen of Sea Grove, NC, kindly donated as much hardwood sawdust as I could haul back to Chapel Hill in my Sentra.

Financial support was provided by the National Science Foundation, Sigma Xi, the UNC Department of Biology, and the UNC Graduate School.

Finally, I thank my parents, Cathy and Dale, for always encouraging scholarship and supporting me whatever I wished to do; and my wife Genevieve and daughter Echo for providing a constant reminder of where true happiness lies.

PREFACE

Perhaps more than any other area of science at any time in history, ecologists at the beginning of the 21st Century are working in what has been called a "doomsday discipline". By many accounts we are in the early phase of a period of mass extinction, the likes of which the earth hasn't experienced for 65 million years, which threatens to rob us of the very objects we study, be it genes, populations, communities, or ecosystems. In large part, this predicament stems from the rising sustenance demands of the exploding human population, which is eroding the biodiversity and environmental integrity of sensitive habitats worldwide. As ecosystems lose species, will they continue to provide the services we require of them? How are we to feed the expected 10 billion people worldwide by 2050 without irreconcilably destroying the basis of global food production?

These two crises—the comparatively rapid loss of species from ecosystems and the need for more sustainable agricultural practices—are united by more than cause and effect. They both beg a seemingly straightforward question: Is biodiversity—the number of species in an ecosystem—related to ecosystem functioning? Plant communities, as the principal provider of humanity's food, fiber, and fuel, represent the basic trophic level at which to begin to ask this question, and productivity, the rate of at which ecosystems fix carbon, is an ecosystem function of obvious significance to humanity. Does the number of plant species in an ecosystem influence its productivity? Or, split up into more well

defined components: are agricultural assemblages with more species more productive, and as ecosystems lose plant species, will other species be able to fully compensate for the lost contribution to ecosystem productivity? There is a long history in plant ecology of modeling both diversity and productivity as a response to environmental conditions; does this mean that these putative diversity-productivity relationships change with environment? This dissertation is largely a detailed treatment of this last question.

This dissertation is only one small part of a research arena with a long history and a flurry of contemporary activity. Indeed, the relationship between species diversity and ecosystem functioning, and the publicity of what has been called the "diversity debate," have garnered the attention of so many researchers that no one researcher is able to absorb and apprehend all the advances in this rapidly developing field. I can therefore only provide a small and incomplete picture of these advances in this dissertation, and, consequently, I focus on a small subset of ideas relating to interactions among diversity, productivity, and environmental factors.

In Chapter 1, I provide a brief introduction to what I call "The ecology of numbers," or the notion that ecosystem functioning is somehow related to the number of objects within it. I see this idea manifest in two, weakly separated lines of investigation, one focused on how ecosystem functioning might be *maintained* with diversity, the other on how ecosystem functioning might be *maximized* by means of diversity. This distinction is roughly represented by the extinction- vs. agriculture-focused questions posed above. In Chapter 2, I present the basic mechanistic hypotheses that guide the rest of this thesis, and focus directly on the relationship between plant species diversity and ecosystem productivity. This includes a detailed discussion of the basic mechanisms of

how plant diversity may influence local ecosystem productivity. I then explore how these mechanisms should be sensitive to certain environmental factors, which in turn suggests certain habitats where the effect of diversity on productivity should be most prominent.

Chapter 3 contains a description and analysis of the first field experiment I conducted to explore several of the hypotheses in Chapter 2. This experiment focused on the relative effects of environmental factors and species diversity on productivity, and resulted in an interesting interaction between soil fertility and species diversity in the control of productivity. This interaction becomes the focus of Chapter 4, which details a second field experiment in which I used both fertility and shading treatments to explore the sensitivity of diversity effects to environment. This study also critically explores several new techniques available for the analysis of biodiversity experiments.

In Chapter 5, I deviate from the experimental approach to seek a more general analysis of the relationship between diversity and productivity, using models of plant competition and species coexistence. I begin by describing biodiversity experiments in terms of a phenomenological species interaction model, and then explicitly add competition for resources to the mix to make predictions of diversity effects over resource gradients. Predictions of biodiversity effects in scenarios where species coexist at equilibrium by means of resource partitioning are compared to those in scenarios away from equilibrium, where species coexist due to intermediate disturbances. I conclude by suggesting that the "complementarity" versus "sampling effect" mechanistic distinction of biodiversity effects is only the latest manifestation of a long-standing "dual" niche concept in ecology. This concept recognizes two basic ways of describing species:

according to their resource requirements, relating to complementarity, versus their environmental impacts, relating to sampling effects.

TABLE OF CONTENTS

LIST OF TABLES xiv

LIST OF FIGURES xvi

Chapter

1. Introduction: A brief history of species diversity as an ecological cause.....1

Intercropping: ecosystem effects at the low end of diversity 2

The ecology of numbers.....4

To maximize or maintain ecosystem function? 7

Maintenance of ecosystem function.....8

Maximization of ecosystem function.....11

Why is the maintenance-maximization distinction important? 13

2. The influence of species diversity on ecosystem productivity: how, where, and why? 18

Abstract.....18

Introduction.....19

How species diversity may influence productivity 22

Complementarity.....23

Facilitation 25

Sampling effect 28

Is the sampling effect an artifact or the analogue of an important natural process?.....30

Variation in sampling effect importance with natural gradients of stochastic community assembly 32

The distinction between local diversity
and species pool diversity 35
Separating the sampling effect and other mechanisms:
the use and misuse of overyielding 38
In what context does diversity or composition influence
ecosystem productivity? 44
Conclusion: why worry about species diversity and productivity
in non-agricultural ecosystems? 47
3. Experiment I: Diversity, productivity, and resource availability 57
Abstract 57
Introduction 58
Methods 60
Results 64
Discussion 66
4. Experiment II: Diversity effects on productivity under different fertility and light conditions 79
Abstract 79
Introduction 80
Methods 83
Experimental design and construction 83
Data analysis 86
Results 89
Absolute effects of diversity and environmental treatments
on productivity 89
Effects of species composition vs. species richness
and species identity 90
Composition and richness: initial treatments vs. realized values ..91
Additive partition of biodiversity effects 92
Dominance, sampling effects, and environment 93
Discussion 94
Facilitation vs. light partitioning 96

Relevance to natural and agricultural ecosystems 98
Future directions 100
5. Plant interaction models, biodiversity effects, and the niche concept.....114
Abstract 114
Introduction 115
Non-mechanistic plant interaction: biodiversity effects and competitive coefficients 118
The interaction matrix and mechanisms of biodiversity effects ..119
Biodiversity effects and interaction reciprocity 122
Biodiversity effects and higher-order interactions.....125
Competition for resources: resource ratios and consumption vectors 127
The basic resource ratio model 128
Biodiversity effects along resource gradients under stable coexistence 130
Biodiversity effects along resource gradients under species dominance 131
Summary of resource ratio model predictions 133
Biodiversity effects away from equilibrium 135
Biodiversity effects, niche theory, and patterns of extinction 140
Conclusion 146
6. Appendix A: Analytical solution of the "cancellation effect" of competition and complementarity in the hyperbolic competition model 156
7. Appendix B: Equations and parameters of simulations in Chapter 5 159
8. References 161

LIST OF TABLES

Table 1.1 Major aspects that differentiate studies of the effect of species diversity on the maintenance of ecosystem function versus the maximization of function 16

Table 2.1 Illustration of the species size-disparity dependence of transgressive and non-transgressive overyielding 51

Table 3.1 Species of the experimental species pool (Experiment I) 72

Table 3.2 Summary tables for two Type I SS ANOVA models describing treatment effects on total aboveground biomass (Experiment I) 73

Table 4.1 Species of the experimental species pool listed in descending order of monoculture yield (Experiment II) 101

Table 4.2 Plant community compositions at each experimental level of species diversity (Experiment II) 102

Table 4.3 Type I SS ANOVA for main treatment effects and interactions on aboveground productivity (Experiment II) 103

Table 4.4 Four Type I SS ANOVA models evaluating relationships between effects of initial and realized composition and richness on productivity 103

Table 4.5 Type I SS ANOVA tables for the additive partition metrics (complementarity, sampling, and net biodiversity effects) in response to mixture richness, environmental treatments, and their interaction 104

Table 4.6 Mean relative yields for each species (except SAHO) in high fertility, shaded and high fertility, full sun environments, arranged in order of tallest to shortest height in mixture 105

Table 5.1 Suggested definitions of interspecific interactions based on the interaction coefficients (alphas) of two hypothetical species 148

LIST OF FIGURES

Figure 1.1 Species diversity and the maintenance versus maximization of ecosystem function 17

Figure 2.1 Two dimensions of species niche distributions play a role in sampling effects—the habitat SE and performance SE—and their importance is determined by environmental conditions 52

Figure 2.2 Factors that influence ecosystem productivity 53

Figure 2.3 Illustration of the two types of overyielding 54

Figure 2.4A Expected niche distributions of species along a resource gradient 55

Figure 2.4B Predicted distributions of the importance of the habitat sampling effect and the performance sampling effect along a resource gradient in randomly-assembled diversity experiments 55

Figure 2.5A Expected niche distributions of species along a regulator gradient 56

Figure 2.5B Predicted distributions of the importance of the habitat sampling effect and the performance sampling effect along a regulator gradient in randomly-assembled diversity experiments 56

Figure 3.1 Magnitudes of effect for significant factors predicting total aboveground biomass 74

Figure 3.2 The interaction between sown species diversity and soil fertility in the control of total aboveground biomass 75

Figure 3.3 Sampling effects in plant mixtures among fertility levels, as calculated by the "selection effect" technique of Loreau and Hector (2001) 76

Figure 3.4 Magnitudes of effect for the presence or absence of certain species separated into three fertility treatments.....77

Figure 3.5 Overyielding in plant mixtures among fertility levels, as calculated by the Relative Yield Total 78

Figure 4.1 Ecological meanings of the complementarity and sampling effects.....106

Figure 4.2 The effect of species richness on aboveground biomass in each of the four unique environments created by low and high soil nutrient levels and full sun and shaded light treatments 107

Figure 4.3 Variation in aboveground biomass explained by different components of species composition, listed as proportion of total composition sum of squares explained by a component 108

Figure 4.4 Non-metric multidimensional scaling ordination of final species composition for all plots, weighted by abundance of *A. hypochondriacus* 109

Figure 4.5 Mean monoculture biomass of each species in each of the four environmental treatments.....110

Figure 4.6 The effect of initial richness of mixtures (2 or 6) on complementarity, sampling, and net biodiversity effects 111

Figure 4.7 Complementarity, sampling, and net biodiversity effects summarized by environmental treatment 112

Figure 4.8 Relative yields (specific mixture mass / monoculture mass) for each species in each of the four environmental treatments 113

Figure 4.9 The relationship between sampling and complementarity effects for all mixtures 114

Figure 5.1 The relationship between mean alpha value of the community matrix and the net biodiversity effect of the mixture for mixtures of 10, 5, and 2 species 149

Figure 5.2 The effect of a reciprocal competitive relationship on the biodiversity effect of two species of equal monoculture value in a simulated "biodiversity" experiment 150

Figure 5.3 The two major species traits of the resource ratio competition model 151

Figure 5.4 Contour graphs of complementarity, sampling, and net biodiversity effects for a two-species resource competition model meeting the conditions of stable coexistence 152

Figure 5.5 Contour graphs of sampling effects for a two-species resource competition model where one species "wins" 153

Figure 5.6 Predicted biodiversity effects on yield along a rate of competitive displacement gradient in a dynamic Lotka-Volterra competition model with intermediate disturbance frequency and no resource partitioning ... 154

Figure 5.7 Complementarity, sampling, and net biodiversity effects for a non-equilibrium Lotka-Volterra model of six-species competition where species partition resources 155

Figure 6.1 The actual relationship between pairwise competition coefficients that produces a "cancellation effect" of competition and complementarity versus the true reciprocal relationship 158

Chapter 1

Introduction:

A brief history of species diversity as an ecological cause

You shall not sow your vineyard with two kinds of seed, or all the produce of the seed which you have sown and the increase of the vineyard will become defiled.
Deuteronomy 22:9

It has been experimentally proved, that if a plot of ground sown with one species of grass, and a similar plot be sown with several distinct genera of grasses, a greater number of plants and a greater weight of dry herbage can thus be raised.
Charles Darwin, *On the Origin of Species*, 1st Ed., p. 113

The moral if not practical consequences of species diversity in ecological assemblages have been appreciated since at least biblical times, and as an ecological question the theme can be traced back to Charles Darwin (fitting the mold of many significant questions in biology). The above passage, appearing first in 1859, has been used several times to add legitimacy to the notion that species diversity and productivity are related (Tilman et al. 1996, Naeem et al. 1999b, Tilman 1999, Hector 2000). This practice led Grime (2001) to take a detailed look at the full passage from which the above quote was taken (Chapter 4, within the subheading "Divergence of Character"). The passage reveals that, although Darwin's comment has been taken to mean that species diversity enhances productivity because species are *ecologically* diverse, Darwin's point actually concerned evolutionary patterns. Indeed, Darwin appears to more closely anticipate Ludwig's (1950) concept of "annidation," where the productivity of

populations tends to increase *over evolutionary time* due to natural selection for traits that allow the harvest of unused resources, later documented in populations of fruit flies (Ayala 1968; see also Antonovics 1978). Grime concludes,

> To state that 'Darwin suggested that greater plant diversity would lead to greater primary productivity, but his thoughts lay dormant for over a century' (Tilman 1999) is to overstate Darwin's observations and to disregard the very considerable research achievements of several subsequent generations of agricultural and ecological research scientists in many parts of the world.

Thus, although it is fair to say that Darwin actually believed that more diverse plant assemblages could outyield less diverse assemblages, he only mentioned it as hearsay, and it is surely an overstatement to say that Darwin's contribution to this topic should carry the same weight as his other historic contributions to biology.[1]

Intercropping: ecosystem effects at the low end of diversity

Worldwide, intercropping, or the growing of two or more crop species together in the same place at the same time, is quite common, and until relatively recently was rather widespread even in North America (Vandermeer 1989). It can therefore be said that, long before the putative relationship between species diversity and ecosystem function entered into the realm of academic ecology, it

[1] Remarkably, the uncited experiment to which Darwin was referring was rediscovered while this chapter was being written. Hector and Hooper (2002) uncovered the missing reference in a later version of Darwin's *Natural Selection* that was not fully published until 1975 (Stauffer 1975), describing experiments conducted by the Duke of Bedford's head gardener, George Sinclair, in Bedfordshire, England, and published originally in *Hortus Gramineus Woburnensis* in 1816. Unfortunately, although Sinclair reported that plots of speciose, transplanted turf were more productive than less diverse plots established from seed, modern experimental methods had not yet been invented and it is impossible to discern whether the higher productivity resulted from transplantation vs. seeding or just certain highly productive species in the turf. Nonetheless, Hector and Hooper suggest that this may be the world's first ecological experiment.

was a historically-tested fact that species diversity, at least the levels immediately above the typical crop monoculture, enhanced many aspects of agriculture, chief among them yearly production per unit of land. The mechanisms behind these yield advantages have been explored in detail over many decades, and often include more efficient use of soil and light resources (Trenbath 1976, Allen et al. 1976), nitrogen fixation by intercropping especially with legumes (Walker et al. 1954, de Wit et al. 1966, Jolliffe 1997), reduced pest and pathogen loads (Andow 1991), and creation of particular microenvironments favorable to particular species (Morgan et al. 1992), among many others. Crop assemblages that perform better than their component monocultures are said to *overyield* (Trenbath 1974, 1976), a concept with solid grounding in the plant competition literature (de Wit 1960). In general, the intercropping literature has been slow to become assimilated into the mainstream ecological literature, although a great leap forward occurred as the result of Vandermeer's 1989 text and agricultural production is on the agenda of ecologists within the diversity-ecosystem function research arena (CAST 1999).

For the questions addressed in this thesis, the important principle derived from intercropping research is that there is no knowledge gained, scientifically or practically, by asserting that small-scale productivity is enhanced by adding certain species to monocultures—not just any species, and not necessarily more than one or a few species (Swift and Anderson 1994, Altieri 1999). In other words, ecology can only contribute to this knowledge base by determining whether levels of diversity higher than a few complementary species further

enhance productivity. In other words, is *number of species* always or often correlated with certain mechanistic phenomena, such as diversification of resource-use traits, that enhance the harvesting of resources from the environment, or do certain processes, such as competitive dominance, prevent such phenomena? Species richness cannot be truly said to influence productivity if high levels of richness are no more productive than 2 or 3 species, or if richness only operates through the properties of certain species.

The ecology of numbers

The putative link between species diversity and ecosystem functioning entered mainstream academic ecology as a stability question and has flourished as such ever since. The origin of this discussion is largely attributed to the work of Robert MacArthur, who in 1955 suggested that systems of fewer linkages between species were more susceptible to population fluctuations. From a slightly different perspective, Elton (1958) famously suggested that "the balance of relatively simple communities of plants and animals is more easily upset than that of richer ones," which became the basis for his hypothesis that more species-rich communities were less susceptible to invasion, a viewpoint subsequently supported by much theoretical research (MacArthur 1970, 1972, May and MacArthur 1972) and still widespread today (Lodge 1993, Levine and D'Antonio 1999; but see Huston and DeAngelis 1994, Lonsdale 1999, Stohlgren et al. 1999, Brown and Peet, in press).

The idea that diversity begets stability was turned on its head by Robert May (1973), who showed that stability, measured in terms of the stability of individual populations, actually decreased with increased diversity (or more particularly "complexity," the number of linkages within a species assemblage). More recently, Tilman (1996, 1999) has pointed out that this view should be restricted to population stability (as May intended), and that stability properties associated with single-trophic communities, such as the temporal variation of total biomass, are expected to increase with diversity. Indeed, the diversity-stability question has recently received much empirical and theoretical attention and mechanisms governing the diversity-stability relationship have been hotly debated (e.g., Naeem and Li 1997, Yachi and Loreau 1999, McGrady-Steed et al. 1997, Doak et al. 1998, Hughes and Roughgarden 2000, Wardle et al. 2000, Kinzig et al. 2002).

The notion that species diversity might influence aspects of ecosystem function not related to stability but rather more immediate processes such as annual biomass production (often called "static" processes; Schlapfer and Schmid 1999) is probably a result of initial worries about the effects massive species extinctions would have on ecosystems and human civilization. The popularity of this perspective is largely attributable to Paul and Anne Ehrlich's 1981 book *Extinction*. In it, the authors argue that the basic life-supporting processes that species perform, such as biomass production, maintenance of air, water, and land quality, climate amelioration, and waste and nutrient recycling, are dependent upon diversity like the functioning of an airplane is to rivets in its wings—the loss

of any one or few species has little consequence, but at some unpredictable level of species loss ecosystem functioning will crash. Since it isn't known how many species an ecosystem requires to function, any species loss could harbor grave consequences. This hypothesis has since become known as the "rivet hypothesis" (Johnson et al. 1996).

It was more than a decade before the rivet hypothesis was experimentally examined using communities of different levels of species diversity, in the microcosm experiments of Naeem and colleagues (1994, 1995) and the semi-natural grassland communities of Tilman and colleagues (1996). These researchers suggested, supposedly for the first time since Darwin (ignoring the intercropping literature), that, because species use resources in different ways, more diverse communities could enhance ecosystem functioning (especially productivity and nutrient cycling) by harvesting more resources from the environment. Since these experiments, research into the relationship between species diversity and (static) ecosystem functioning has exploded, and a heated controversy has developed that has come to be known as the "diversity debate" (Kaiser 2000).

The diversity debate lies at the heart of this dissertation and the various sources of contention will be introduced in Chapter 2. When distilled down to its basics, the true nature of the controversy is a debate over *numbers*. That is, can ecosystem functioning be related to the number of objects within it? Or is it some other aspect of species diversity that matters, such as the traits of certain species, the many factors (such as environment) that determine diversity in the first place,

or larger functional aspects (such as trophic complexity) that are correlated with overall species diversity? Because species traits, environmental factors, and functional complexity are all well known as factors that influence ecosystem function, those on one side of the debate don't understand why "species diversity" per se is getting all the attention. The view of the protagonists on the other side can perhaps be best represented by a statement from Tilman's (1999) MacArthur Award Lecture: "Diversity must be added to composition, disturbance, nutrient supply dynamics, and climate as a determinant of ecosystem structure and dynamics." That is, among all the factors that influence ecosystem function, *number of species* has effects of the same order of magnitude. The experiment detailed in Chapter 3 of this dissertation is, in a sense, a reply to this assertion.

To maximize or maintain ecosystem function?

Before narrowing the focus of this thesis to species diversity and ecosystem productivity, it is useful to briefly summarize the current research relating to ecosystem function in order to put the diversity-productivity relationship in the context of a much larger research agenda. I suggest that an effective way to organize the many different approaches is for researchers to distinguish between studies that address the *maintenance* of ecosystem function versus those that address the *maximization* of ecosystem function. Maintenance-of-function studies concern the impact of consecutive species extinctions on the functioning of "intact," often multi-trophic study communities and employ a niche concept and "functional group" approach derived from animal and

ecosystem ecology. Conversely, maximization-of-function studies explore the functional benefits of adding species to an ecosystem, particularly with regard to ecosystem productivity, and typically involve plant communities where species are functionally grouped by their resource requirements. In what follows, I briefly describe the major differences between studies that examine the maintenance of function versus the maximization of function and then explain why this distinction is crucial to the interpretation of studies investigating the diversity-function relationship. Table 1.1 summarizes the major differences between the maintenance and maximization perspectives.

Species diversity and the maintenance of ecosystem function

Studies that approach the diversity-function relationship from the maintenance perspective address the general question: What is the effect of consecutive species extinctions on the functioning of ecosystems? More specifically, these studies concern how relatively intact ecosystems will respond to losses of their constituent species. Relevant dependent variables, often loosely defined, include those that are indicative of the integrity and stability of the ecosystem itself (e.g., ecosystem "reliability" sensu Naeem 1998; ecosystem "health" sensu Rapport et al. 1999) and those that indirectly support human populations (e.g., ecosystem "goods and services" sensu Ehrlich and Ehrlich 1981). Because many researchers of maintenance-based studies have had backgrounds in animal, microbial, or ecosystem ecology, their study communities are often multi-trophic and composed of trophic-based "functional groups" that

represent an ecosystem's basic, functionally linked biotic compartments (autotrophs, herbivores, predators, decomposers). Within these groups, species interactions are addressed from the perspective of "compensatory" dynamics, where functional loss due to extinction (or simply decreased abundance) of one species is adequately replaced by the functional contribution of another species within the group, leading to "homeostasis" (i.e., maintenance) of that ecosystem function (e.g., Frost et al. 1995, Klug et al. 2000, Ernst and Brown 2001). To the extent that compensatory dynamics causing homeostasis occur within a functional group if species are removed, species within groups may be said to be "redundant" (Walker 1992, Lawton and Brown 1994, Naeem 1998). Not surprisingly, such species categorizations reflect a niche concept derived from Elton (1927) in that species are defined by their functional roles and trophic positions (see also Whittaker et al. 1973, Leibold 1995), a distinctly different approach to species categorization than that used by researchers studying the maximization of ecosystem function described below.

Because maintenance-of-function studies inform how natural ecosystems respond to species extinction, it is important that they use species that have historically co-occurred in ecological communities and employ diversity gradients created by consecutive species removals rather than purely random assemblages (Petchey 2000). Indeed, a pertinent example of the confusion between the maintenance and maximization perspectives is the debate over proper experimental designs in studies of the importance of diversity for ecosystem function. Both Huston (1997) and Wardle (1998) have criticized microcosm

experiments of Naeem and colleagues (Naeem et al. 1994, Naeem and Li 1997, respectively) for constructing species diversity gradients as compositional subsets of the most diverse treatment because they potentially confound species diversity with species composition. From a maintenance perspective of ecosystem function, however, this design is appropriate because it mimics how species extinctions will potentially impact the functioning of intact ecosystems. Indeed, more relevant concerns are whether the initial construction of the "intact" (most species-rich) microcosm communities is an adequate approximation of how communities are assembled in natural ecosystems, particularly with regard to mutualistic assembly rules and coevolutionary relationships (Rastetter et al. 1999), and whether real patterns of extinction are approximated.

Two major conclusions have emerged from studies of the maintenance of ecosystem function in response to species extinction. Ecosystems are more robust to functional loss if species redundancy is high—that is, if there are many species within functional groups that can functionally compensate for one another (Walker 1992, Lawton and Brown 1994, Naeem and Li 1997, Naeem 1998, Griffiths et al. 2000, Nijs and Impens 2000). Conversely, ecosystem function is more sensitive to species loss with increasing functional diversity—that is, the greater the number of functional groups, or the larger the range of functions represented by a group of species, the more likely a portion of ecosystem function is lost with each species extinction (Naeem 1998, Nijs and Impens 2000). An "ideal" ecosystem from the standpoint of the maintenance of its function would include high levels of species redundancy but low levels of functional diversity.

At the extreme, a community of functionally equivalent species would exhibit the maximum robustness to functional loss resulting from species extinction.

Although multi-trophic communities compose the vast majority of studies that address ecosystem function from the maintenance perspective, maintenance-of-function studies may be based on the functioning of any type of ecological assemblage. Experimental plant communities in particular have been used to demonstrate the relationship between species diversity and ecosystem- and community-level measures of stability (e.g., McNaughton 1977, Leps et al. 1982, Tilman and Downing 1994, Tilman 1996, Walker et al. 1999). To the extent that such studies compare the stability measures of more "intact" assemblages with those of more species-poor compositional subsets, they are primarily addressing the role of species diversity in maintaining ecosystem function.

Species diversity and the maximization of ecosystem function

Studies that approach the diversity-function relationship from the maximization perspective address the general question: Do ecosystems of greater species diversity generally exhibit higher levels of ecosystem function than those less diverse? These studies specifically seek to determine how species diversity might be used to enhance ecosystem function, particularly with regard to ecosystem productivity (Tilman et al. 1996, Naeem et al. 1996, Tilman et al. 1997, Hector et al. 1999, Fridley 2001), nutrient cycling (Tilman et al. 1996, Hooper and Vitousek 1997), and combating species invasion (e.g., Lavorel et al. 1999). Plant ecologists and agriculturists have been at the forefront of this type of

research, largely due to the central global importance of maximizing agricultural production (Swift and Anderson 1994, CAST 1999). Species in these studies are also classified into functional groups, but groups are defined within a trophic level, are self-sufficient, and are largely based on resource acquisition (Vitousek and Hooper 1993, Smith et al. 1997, Hooper 1998), reflecting a niche concept closer to that of Grinnell (1917) who described species according to their resource requirements (corresponding to the "habitat" of Whittaker et al. 1973 and the "requirement niche" of Leibold 1995). The single-trophic perspective also translates into a larger emphasis on competition and facilitation (Hooper 1998, Fridley 2001) rather than species compensation and redundancy. Moreover, because the maximization of ecosystem function is concerned more with anthropocentric values than the integrity of natural ecosystems (defined loosely as the persistence of composition and system processes), the use of co-evolved or naturally co-occurring species is unnecessary.

Experimental grassland communities constitute a large portion of studies conducted on the ability of species diversity to maximize ecosystem function (Tilman et al. 1996, Hooper and Vitousek 1998, Hooper 1998, Symstad et al. 1998, Hector et al. 1999, Naeem et al. 1999a). The overriding conclusion of the studies is that the relationship between species diversity and ecosystem function is strongly dependent upon how much functional or ecological diversity a certain group of species represents (Naeem et al. 1999b, Tilman et al. 1997a, Tilman 1999). More particularly, it has been found that ecosystem function is more dependent on functional group diversity than species diversity (Tilman et al.

1997b, Hooper 1998, Hector et al. 1999). In other words, when ecosystem function is to be maximized by means of species diversity, it is most desirable that species represent a maximal amount of functional diversity so that each added species performs a unique function.

Why is the maintenance-maximization distinction important?

The separation of diversity-function studies into those that seek to maintain versus maximize ecosystem function is crucial to their interpretation because it requires changes in species diversity to be evaluated from opposite sides of the diversity-function curve (Figure 1.1). If ecosystem function is to be maintained, diversity and function begin at their maxima and *decline*; if function is to be maximized, diversity and function begin at zero and *increase*. In this context, the very components of species diversity that are desirable in maintaining function are those undesirable in maximizing function. This is because when function is to be maintained under species extinction, one wants species as identical as possible so that no function is lost with species loss. That is, one is not as concerned with the actual level of ecosystem function in the most species-rich treatment as with the drop in function with species loss. In contrast, when function is to be maximized, one wants each species to be as functionally distinct as possible so that each addition has ecological meaning. Put another way, from the maintenance perspective, the most ideal diversity-function curve would be a flat line; from the maximization perspective, the most ideal curve would be a steep increasing function.

Aspects of diversity that render species functionally unique, such as niche differentiation, are desirable from the perspective of an agricultural producer who seeks to enhance production through the use of diversity, but undesirable from the perspective of a manager trying to maintain the integrity of an ecosystem prone to species loss. In the same way, species redundancy renders ecosystem function more robust to species loss, but does not allow for further enhancement of ecosystem function. In other words, species redundancy always reduces the *sensitivity* of ecosystem function to changes in species diversity, but whether redundancy is of "benefit" to ecosystems depends on whether their function is to be maintained or maximized. Similarly, functional diversity always increases the sensitivity of ecosystem function to changes in species diversity, but whether high functional diversity is a desired attribute of ecosystems depends on whether species are being added or removed. It will always be more difficult to maintain the services of an ecosystem in response to species extinction when species diversity represents a high degree of functional diversity. Therefore, studies of the relationship between species diversity and ecosystem function must adequately address the maintenance-maximization distinction before concluding which aspects of species diversity are "beneficial" to ecosystem function for any particular study system.

Both maintenance- and maximization-based studies are necessary if ecological research is to be the driving component behind the management of ecological systems. Just as it is crucially important that ecologists provide robust strategies for maintaining the functioning of natural ecosystems in response to

widespread species extinctions, ecologists should be at the forefront of finding ways to further enhance agricultural production and sustainability, particularly in response to the changing environmental conditions brought about by climate change, chemical pollutants, and other anthropogenic threats to diversity and ecosystem function.

The maintenance of function perspective, which is generally aimed at a multi-trophic level approach to the biodiversity-function relationship, will emerge later in Chapter 5. For the most part, this thesis will deal most immediately with whether or not species diversity can help maximize ecosystem productivity, manifest especially in the experimental designs of Chapters 3 and 4. As such, the field experiments detailed in those chapters are of most immediate relevance to agricultural systems where both productivity and maximization are the most important concerns.

Table 1.1. Major aspects that differentiate studies of the effect of species diversity on the maintenance of ecosystem function versus the maximization of function. Listed differences are only meant to provide a general characterization of the maintenance-maximization distinction and are not strict categorizations.

Aspect	**Maintenance**	**Maximization**
Dependent variables	Ecosystem services, health, integrity, reliability, stability	Productivity, nutrient retention, invasibility
Ideal study systems	Intact natural ecosystems	Field experiments
Typical researchers	Animal, ecosystem ecologists	Plant ecologists, agriculturists
Niche concept	Eltonian: species' functional role	Grinnellian: species' habitat space
Functional group usage	Multi-trophic and linked (Naeem 1998)	Uni-trophic and self-sufficient (Hooper 1998)
Important species relationships	Compensation and redundancy	Complementarity and facilitation
Diversity gradient	Consecutive species removals	Species addition
Species pool	Co-evolved and co-occurring	No constraints
Most direct applications	Conservation	Agriculture
Representative studies	Ehrlich and Ehrlich 1981, Walker 1992, Naeem 1998	Tilman et al. 1996, Hooper 1998, Hector et al. 1999

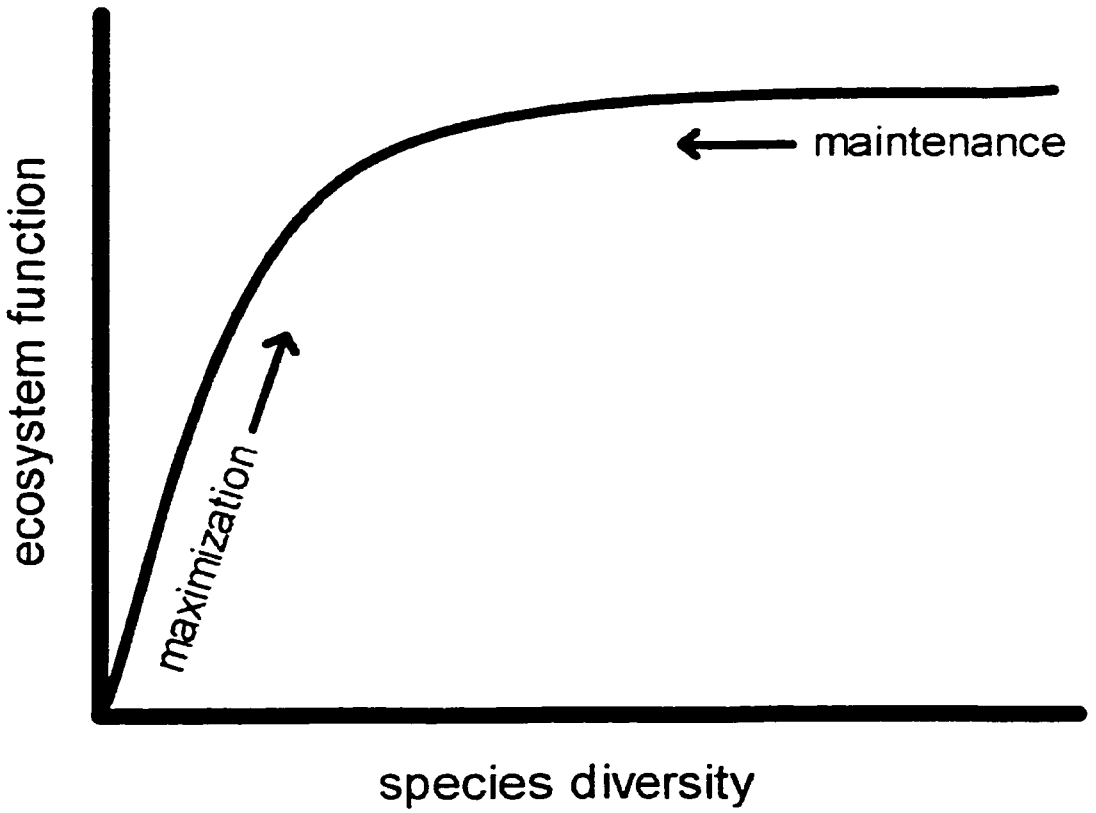

Figure 1.1. Studies concerned with the maintenance of ecosystem function in response to loss of species diversity begin at the upper end of the diversity-function curve; those concerned with the maximization of function add species and function from the lower end.

Chapter 2

The influence of species diversity on ecosystem productivity: how, where, and why?

Abstract

The effect of species diversity on ecosystem productivity is controversial, in large part because field experiments investigating this relationship have been fraught with difficulties. Unfortunately, there are few guidelines to aid researchers who must overcome these difficulties and determine whether global species losses seriously threaten the ecological and economic bases of terrestrial ecosystems. In response, I offer a set of hypotheses that describe *how* diversity might influence productivity in plant communities based on three well-known mechanisms: complementarity, facilitation, and the sampling effect. Emphasis on these mechanisms reveals the sensitivity of any diversity-productivity relationship to ecological context (i.e., *where* this relationship should be found); ecological context includes characteristics of the surrounding environment, temporal and spatial scales of observation, and the intensity of human management. In particular, the legitimacy of the sampling effect as a mechanism of productivity enhancement is dependent upon the degree to which stochastic events influence immigration and extinction processes in a given ecosystem. A mechanistic approach also requires that the three mechanisms be separated and quantified in diversity experiments, and I examine the most appropriate analyses for doing so,

focusing on the overyielding technique. Finally, I question *why* productivity per se is a relevant management concern in non-agricultural systems once relationships among diversity, productivity, and the qualities of the surrounding environment are considered.

Introduction

"Debate among ecologists over the importance of biodiversity to the health of ecosystems has erupted into a full-blown war."

News Focus, *Science*, 25 August 2000

Ecosystem productivity, the rate of whole-ecosystem biomass production, is influenced by the identities of the species that comprise an ecosystem. But does the number of species in an ecosystem affect productivity? Researchers studying plant communities of artificial microcosms (Naeem et al. 1994, Naeem et al. 1995, Symstad et al. 1998, Engelhardt and Ritchie 2001) and semi-natural grasslands (Naeem et al. 1996, Tilman et al. 1996, Tilman et al. 1997b, Hector et al. 1999, Tilman et al. 2001) have asserted that species diversity influences ecosystem properties, especially productivity (Loreau 1998a, Tilman 1999a, Naeem et al. 1999, Loreau 2000, Loreau et al. 2001). However, these studies have generated a considerable amount of criticism based upon their experimental methodology (Huston 1997, Hodgson et al. 1998, Wardle 1999), analyses (Aarssen 1997, Huston et al. 2000), and general conclusions (Grime 1998, Wardle et al. 2000, Grime 2001). Indeed, there remains more disagreement than agreement among researchers actively studying the relationship between diversity

and productivity, despite claims to the contrary (Loreau et al. 2001), with the result of no clear consensus of if or how diversity influences productivity.

One cause of the diversity-productivity debate, and a reason that this relationship remains controversial, is the lack of clear hypotheses to guide experimental hypothesis testing. For example, what qualifies as an effect of diversity? Inevitably, in experiments of treatments of varying species richness levels, those plots initially more diverse are more likely to contain certain species whose presence more greatly affects plot productivity than others in the species pool—a phenomenon called the "sampling effect." Should the sampling effect qualify as a diversity effect, or is it an undesired artifact of experimental methodology? As a genuine mechanism of a diversity effect, the sampling effect has been both defended (Tilman et al. 1997a, Naeem et al. 1999, Tilman 1999a, Loreau 2000) and disputed (Aarssen 1997, Huston 1997, Garnier et al. 1997, Wardle 1999, Huston et al. 2000, Wardle et al. 2000). If the sampling effect is regarded as an experimental artifact, how should this artifact be removed? This too has been debated (Garnier et al. 1997, Hector 1998, Loreau 1998b, Huston et al. 2000, Loreau 2000, Loreau and Hector 2001) and the measurement of overyielding, which seeks to quantify the true extent of crop mixture advantage (de Wit 1960, Trenbath 1976, Vandermeer 1989), has emerged as a valuable analysis tool, along with more recent statistical treatments (e.g., Loreau and Hector 2001). Nevertheless, researchers are still lacking criteria to decide whether there are some cases where sampling effects may be relevant in natural ecosystems.

The difficulties involved in testing hypotheses of a diversity-productivity relationship are compounded by the shortage of specific mechanistic models describing how a greater number of species might enhance productivity, given the obvious roles of species identity and the qualities of the surrounding environment. Without such models, researchers are stuck trying to fit general phenomenological models to systems of a wide variety of ecological contexts. It will almost certainly be more profitable for researchers to focus on ways in which certain ecological circumstances allow species diversity to govern ecosystem productivity rather than pursue a single, universal relationship between diversity and productivity. In other words, by providing researchers with potential mechanisms by which diversity may affect productivity, and specifying the ecological contexts in which these mechanisms may operate, a pluralistic perspective allows experimenters to more robustly test hypotheses of the relationship between diversity and productivity. This approach also better suits the needs of ecosystem managers who operate under a particular set of environmental and ecological contexts.

In response to the need for a more mechanistic framework describing the diversity-productivity relationship, I suggest that the processes governing species interaction and community assembly, including competition and facilitation, allow diversity to promote productivity by means of three general mechanisms: complementarity, facilitation, and the sampling effect. I briefly summarize what is known about complementarity and facilitation and recast the sampling effect as a complex phenomenon that is closely tied to the degree to which stochastic

events influence species immigration and extinction. This reformulation of the sampling effect allows ecological context (e.g., environmental conditions, spatial and temporal scales of observation, human management intensity) to enter the discussion of whether to include the sampling effect as a legitimate effect of diversity on productivity. Because the realized effect of these mechanisms on productivity is dependent upon ecological context, it is necessary to separate their effects in diversity experiments. Appropriate analyses for separating these mechanisms have been suggested, but no consensus has emerged (Garnier et al. 1998, Hector 1998, Loreau 1998b, Huston et al. 2000, Loreau and Hector 2001); I advocate a method for detecting mechanisms of enhanced mixture productivity and attempt to clarify semantic issues concerning the measurement of overyielding. Finally, after exploring the importance of each of the three mechanisms along selected ecological gradients, I explore the general consequences of these hypotheses: In what context does diversity affect productivity? Are species diversity and overyielding related? Does ecological context provide a basis for deciding where ecosystem productivity is a legitimate management concern?

How species diversity may influence productivity

Species diversity may promote ecosystem productivity in three general ways. Complementarity occurs when competition from interspecific neighbors is lower than that from conspecifics as a result of differences in resource requirements, which may lead to more complete use of environmental resources

by a more species-rich community (Loreau 1998a, Hooper 1998). Facilitation occurs when an individual attains greater biomass in the presence of interspecific neighbors because of their beneficial effects on an intermediary resource (defined broadly to include resource enhancement or alleviation of stress or disturbance) (Vandermeer 1989). The sampling effect comprises the greater probability of including more productive species (or combinations of species) in more species-rich communities (Tilman et al. 1997a, Huston 1997). In addition, the sampling effect can involve the greater probability of complementary and facilitative interactions in more species-rich communities. In the following summary of these three potential mechanisms of the diversity effect, I argue that there is little empirical support for a necessary relation between high levels of diversity and complementarity or facilitation, but there is a potential relation between diversity and the sampling effect.

Complementarity

Because it is presumed that competition is the predominant interaction among plant species, an explanation of how species coexist and how they might act concomitantly to influence ecosystem function must focus on how competitive exclusion is avoided. Several influential models of plant species coexistence suggest that coexistence is the result of niche partitioning, or differences in resource requirements among species. Partitioning may include species using different types of resources (e.g., chemical forms of nitrogen), different ratios of amounts of resource types needed (e.g., light-water tradeoffs), or different times

or spaces of exploitation of the same resource (e.g., phenology, rooting zones). More generally, coexisting plants are thought to complement each other in traits related to resource foraging (Tilman 1982, Smith and Huston 1989), life-history strategy (Grubb 1977), or both (Grime 1977). Complementarity is the reduction of interaction due to differences in species traits, or, more specifically, reduced competition between interspecific neighbors, one or each of which would be more greatly suppressed by a conspecific neighbor. Species may "control" productivity via complementarity because resource partitioning enhances total resource use, and thus often a greater amount of energy is harvested in plant mixtures compared to their monocultures (Trenbath 1974, Jolliffe 1997). Indeed, complementarity is the principal basis for the science of intercropping and evidence in support of complementary species associations in agriculture is extensive (Ewel 1986, Willey 1990).

Complementarity is a central principal behind the "functional group" approach in which species diversity is broken down into its most obvious functional components (Tilman et al. 1997b, Hooper 1998). But is complementarity related to species diversity beyond what is expected from the inevitable correlation of functional diversity and species diversity? Though theoretically attractive (e.g., Tilman et al. 1997a), there is no empirical support for a necessary relationship between diversity and complementarity. Complementarity has been found to be the product of particular species combinations, not random species combinations (Tilman et al. 1997b, Hooper and Vitousek 1997, Hooper 1998). Naeem et al. (1994) and Naeem et al. (1995),

describing a trend of enhanced light capture in more diverse plant assemblages, argued that increased diversity produced a greater variety of leaf forms and plant canopies within the community, which led to greater packing of photosynthetic tissues. While this possibility is intuitively appealing, these studies have been criticized for confounding species richness levels with particular species compositions (Huston 1997); it is possible that more efficient light use in the highest diversity treatments was caused by a certain densely-foliated species or, more likely, canopy packing of only a few complementary species. The efficiency of light capture is indeed a common principal in the design of intercropping systems (Allen et al. 1976), but there is little evidence that such light partitioning occurs among all species in communities of more than 3 or 4 species. Thus, species composition, and that of relatively few species, is likely the best predictor of resource partitioning among plant species, not the number of local species (Schwartz et al. 2000). Because few diversity-productivity studies have been constructed to test mechanistic hypotheses, however, these relationships require further exploration.

Facilitation

A robust, mechanistic definition of facilitation for intercropping studies was suggested by Vandermeer (1989), who defined it as the circumstance where a species modifies the environment in a way favorable to a co-occurring species. This definition highlights the typical nature of plant interaction, through an intermediate entity, which could be a resource (e.g., nitrogen, water), a regulation

factor (e.g., temperature, wind stress), space, or interactions with other species or trophic levels (e.g., weeds, herbivores). Examples of facilitative processes in intercropping are numerous (Vandermeer 1989). Requiring facilitation to occur via an intermediate material conceptually separates it from complementarity. Theoretically, this also gives researchers the potential to separate occurrences of the two mechanisms because intermediate materials can be manipulated independently of the effects of neighboring plants.

Current perspectives on the significance of facilitation in structuring plant communities often include beneficial effects among neighboring species of different life stages (Callaway and Walker 1997). For example, large desert perennials or "nurse plants" often aid in the establishment of younger neighbors by alleviating thermal and water stresses (Turner et al. 1966, Fowler 1986). These relationships are also important in managed ecosystems. In Britain, for example, spruce production is enhanced by growing spruce seedlings under the canopy of pines and larches (Morgan et al. 1992). The importance of facilitative relationships via the "nurse plant" mechanism has yet to be addressed in diversity-productivity experiments, however, because experimenters have grown only one cohort of plants. The juxtaposition of several life stages should become a component of future experiments [and is an important part of the experimental designs described in Chapters 3 and 4].

The only facilitative mechanism addressed in diversity-productivity experiments is nutrient enrichment by N-fixers, despite evidence for several other facilitative processes in natural communities, such as water sharing via hydraulic

lift (Caldwell et al. 1998) and nutrient sharing via mycorrhizal networks (Read 1997). Although the presence of N-fixers in certain N-limited habitats is undoubtedly an important mechanism of plant control over ecosystem productivity, the use of N-fixers in experiments may actually confound attempts to explore the relationship between diversity and productivity. For example, Hector et al. (1999) claimed that the number of functional groups (including N-fixing legumes, grasses, and non-leguminous forbs) present was a significant predictor of ecosystem productivity in their experimental grassland plots. However, their data are consistent with an interpretation based on simply the presence or absence of one functional group—N-fixers (Huston et al. 2000; but see Loreau and Hector 2001). Thus, their claim may be an artifact of legume inclusion (an important sampling effect component; see below) rather than an indication of complementarity among functional groups. Indeed, nearly all plant community experiments investigating the functional significance of diversity have included N-fixers as a functional group (e.g., Tilman et al. 1997b, Symstad et al. 1998), leaving open the possibility that the perceived significance of plant functional group diversity for ecosystem function is actually overestimated due to a sampling effect for the N-fixing group. At this point, using N-fixers in experiments appears to create more confusion than understanding of diversity-productivity relations, and there is dire need to perform experiments on the role of functional groups without the confounding presence of N-fixers. Thus, as for the case of complementarity, there is currently no unambiguous evidence suggesting

that random increases in species diversity enhance the strength or frequency of facilitative interactions.

The sampling effect

Although the sampling effect has been discussed primarily in terms of differentially including species of greatest inherent productivity in more diverse plots, it is actually an amalgam of at least four separate phenomena, of which inherent productivity is but one component. These four phenomena can be separated into two that focus exclusively on the traits of the species being selected and two that depend both on these species traits and those of the community to which the species are being added. Concerning traits of the introduced species, the sampling effect can be separated into the greater likelihood of selecting a species 1) better adapted to the particular site conditions, or 2) of higher potential growth rate or larger mature size. The first process—the habitat sampling effect—is that of finding a "match" between species and environment, in the sense of an "environmental filter" (Wilson 1999). "Habitat" is meant to emphasize niche breadth (Figure 1), or the range of a species distribution along a resource gradient (*sensu* Whittaker et al. 1973). The ability of a species to tolerate a range of conditions along a resource gradient has been hypothesized to negatively relate to its maximum potential productivity, or niche amplitude, due to trade-offs between growth rate and stress tolerance (Grime 1977, Chapin 1980, Smith and Huston 1989, Austin and Smith 1989). The second process—the performance sampling effect—is a property of the maximum size or growth rate

of an individual, reflected in its maximum niche response (or amplitude) (Figure 1). Here "performance" refers specifically to vegetative growth of an individual, and thus may not necessarily correlate with fitness. Often growth rate or mature size and competitive ability are correlated, particularly in fertile sites (Grime 1979, but see Newman 1973); the performance sampling effect is thus related to selecting species of greater competitive ability, at least for terrestrial plants. For organisms or habitats in which competitive ability and growth rate are negatively correlated and sufficient competitive exclusion occurs, ecosystem productivity may be reduced by diversity via a similar sampling phenomenon (Tilman 1999b).

The other two sampling effect components are functions of both the traits of the selected species and the community to which species are added. As such, they compose "biotic filters," important aspects of community assembly rules (Wilson 1999). If two species within a species pool highly complement each other, for example, then a mixture that includes these two species might be expected to lead to enhanced productivity and they should stably coexist. The likelihood of pairing these species in mixture increases with the number of species drawn from the species pool (Hooper and Vitousek 1997)—a sampling effect for complementarity. In a similar manner, if a certain species in the species pool has a large facilitative effect on a few or all of the other community members, such as a N-fixer, the likelihood of including this species in a community increases with the number of species drawn (Wardle 1999, Huston et al. 2000)—a sampling effect for a facilitator.

Sampling effects can, in theory, create negative relationships between species diversity and productivity if species that end up dominating mixtures are those which also have lower-than-average monoculture yields (Loreau and Hector 2001; see also Figure 4.1). In terrestrial plant species that occur in environments in which asymmetrical light competition is the most important filter on abundance and species coexistence (where abundant evidence suggests this occurs in a wide variety of habitats not subject to high levels of stress or disturbance; Grime 1972, Huston 1994), negative sampling effects should be rare to nonexistent. This is because the yield of species in monoculture is closely related to competitive ability, or the ability of certain species to dominate mixtures (Al-Mufti et al. 1997, Grime 1977). However, in environments where productivity (or growth rate) and competitive ability (or relative abundance) are negatively related, such as water-stressed environments, negative sampling effects may indeed be important. Another way of stating this hypothesis is that negative sampling effects should be expected to occur whenever the most competitive species (highest competition coefficients) have lower-than-average carrying capacities for a particular environment (Tilman 1999b). This will be discussed in more detail in Chapter 5.

Is the sampling effect an artifact or the analogue of an important natural process?

The crux of the debate over the validity of the sampling effect as a mechanism of the diversity effect is whether the methods of random species addition or deletion used in most diversity experiments are relevant to how

species are added or deleted in non-experimental ecosystems. Obviously, species are not randomly added to agroecosystems or other such managed systems. Natural communities are also not assembled randomly—Watt (1947), Whittaker (1956), and many others illustrated the predictability of community composition along broad successional and environmental gradients long ago (Kershaw 1973). However, it is equally apparent that chance events sometimes play an important role in both species addition processes (immigration) and species deletion processes (extinction) (MacArthur and Wilson 1967, Roughgarden 1989). This is not to say that deterministic and stochastic processes have equal control over vegetation pattern; rather, community composition in a particular ecosystem at a given time is predictable within certain bounds, but this precision varies among ecosystems. If, as an extreme example, future composition (constrained from a species pool) were completely unpredictable, one would wish to include all species to maximize productivity even if one species eventually came to dominate. It is this issue of compositional uncertainty that allows the sampling effect to be a mechanism of productivity enhancement in natural ecosystems. It then follows that the relevance of the sampling effect as a legitimate mechanism of the diversity effect is related to the degree to which immigration and extinction processes are stochastic for an ecosystem of specific environmental position and scale of observation.

Factors that influence the degree to which communities are deterministically or stochastically assembled are not well known and a complete discussion of this topic is not merited here. However, several researchers have

explored the predictability of community composition along specific ecological gradients. It is thus appropriate to consider these examples and how the influence of the sampling effect might also be described along these gradients.

Variation in sampling effect importance with natural gradients of stochastic community assembly

One example of a natural gradient in the relevance of the sampling effect as a mechanism of the diversity effect is that stochastic events influence immigration and extinction processes to a greater degree in smaller areas than in larger areas. It has been empirically shown that the compositional predictability of plant communities increases from small to large sampling areas (Reed et al. 1993). Moreover, van der Maarel and Sykes (1993) introduced the "carousel model" in which many local species in a chalk grassland community colonized available microsites without apparent pattern, and composition in small plots (e.g., 2.5 m^2) was unpredictable and highly unstable from year to year. Indeed, the plot size at which composition appears to have an important stochastic component in herbaceous plant communities is the scale at which nearly all diversity-productivity studies have been conducted (ca. m^2). Therefore, processes akin to sampling effects in experiments appear to be operating in some natural ecosystems, at least for small areas.

A similar gradient of stochasticity appears to be operative along a temporal continuum, whether in terms of biotic change (e.g., succession) or environmental fluctuation. Several researchers, for example, have suggested that

the predictability of species composition increases with time after the onset of succession (Margalef 1963, Kershaw 1973, Peet 1992). For example, del Moral and Wood (1993) reported that composition was largely unpredictable in the first years of primary succession on Mount St. Helens. Given suitably constant environmental conditions, greater compositional predictability though time suggests that the sampling effect will influence plot productivity to a greater extent in earlier measurements of yield, and less so as plot composition converges on a predictable yet dynamic assemblage (Peet 1992). On the other hand, the variance of observed conditions increases with time, and in a fluctuating environment that causes corresponding fluctuations in composition, the sampling effect should become a greater influence on total productivity as the duration of observation increases (and is the opposite of that predicted for increases in spatial area). Thus, in a time interval of relatively stable environment, the role of the sampling effect should decrease with time, but in scenarios of greater environmental fluctuation, the role of the sampling effect should depend upon the relative influences of compositional convergence (from succession) and stochastic environmental change.

Ecosystems can also be placed along a gradient of human management intensity, and stochastic processes are greatly reduced in intensively managed systems. The sampling effect plays little to no role in agricultural systems where the abundances of crop species are highly regulated and random assembly processes are all but eliminated from the management regime. The same is true, although to a lesser degree, in foraged grasslands and forests managed for timber

production. It is incorrect, however, to assume that agricultural management precisely regulates species performance, as agroecosystems vary widely in their complexity and natural autonomy (Swift and Anderson 1993). There are conditions in which a sampling effect process may be significant. For example, crop diversification, and agricultural diversification in general, is deemed enormously important in terms of risk minimization (Vandermeer et al. 1998), and this results from future environment unpredictability—an argument very similar to those involving the importance of biodiversity for buffering productivity in natural ecosystems (Yachi and Loreau 1999, Tilman 1999a). Thus, although the influence of the sampling effect on ecosystem productivity may be small in managed ecosystems in general, it may be more informative to place a given system along a gradient of management intensity, from highly managed ecosystems to relatively stable natural ecosystems to communities generally regarded as highly unstable.

The necessary emphasis on ecological scale in deciding whether the sampling effect is relevant in non-experimental ecosystems becomes especially apparent in the examination of the interaction of regional and local processes governing both species diversity and local ecosystem productivity. At the local or neighborhood scale (say, m^2) and at small temporal scales, productivity may indeed be highly dependent upon which species are there, not how many are there (Aarssen 1997, Huston 1997, Garnier et al. 1997). Which species are present at this scale is a function of environmental conditions, including resource availability and disturbance regime, and the nature and intensity of local biotic

interactions (which in turn are strongly influenced by environment) (Grime 1973, Huston 1979, Grace 1999) (Figure 2). Importantly, however, the composition and diversity of the pool of potential colonizing species ("species pool") also affects local species composition and diversity (Cornell and Lawton 1992, Partel et al. 1996, Cornell 1999, Huston 1999; but see Austin 1999). (As used here, "species pool" is defined as the set of species that may potentially survive in and disperse to a particular community, defined as the "local pool" in Partel et al. 1996). Thus, at the scales at which nearly all diversity experiments have been conducted, there may be little reason to expect local diversity to enhance productivity, but the size and composition of the species pool may affect local production by controlling which species are available for colonization—a process analogous to the experimental sampling effect. By using experimental species richness treatments as treatments of species pool size, however, small-scale diversity-productivity studies have the potential to provide insight into natural "sampling" processes.

The distinction between local diversity and species pool diversity

Species diversity has been most often modeled as responding to site productivity, not affecting it (Grime 1973, Huston 1979, Tilman 1982), and abundant evidence supports a unimodal ("hump-backed") relationship between local species diversity and standing biomass (Grace 1999; but see Waide et al. 1999). The general model illustrated in Figure 2, however, potentially resolves this paradox by recognizing that the two opposite pathways of causation are actually employing two different scales of diversity—local diversity in the case of

the hump-backed model and the diversity of the species pool in the case of the diversity-productivity effect. This is because local diversity is largely a function of local environmental conditions, most notably fertility and disturbance levels as predicted by the hump-backed model. However, a proportion of the variance in total productivity levels among habitats is explained by *which* species are present, and this is in turn a function of the composition and diversity of the species pool. Therefore, a large portion of the variance in local species diversity among habitats is explained by site conditions, manifest as productivity; a smaller portion of the variance in local habitat productivity is explained by local species composition, determined in part by the size of the species pool via the sampling effect. High species pool diversity provides a greater array of species (and species traits) that environments and communities may "select" from; all else equal, diverse species pools are more likely to contain species of higher growth rates than smaller pools and are more likely to contain species better adapted to a greater array of environmental conditions. Therefore, by reducing species pool diversity, global species extinctions weaken the ability of the sampling effect to regulate local productivity (and ecological processes in general), and especially in response to global environmental change that is forcing local biotic communities to quickly adapt to radically new local environments (Bazzaz 1996).

Rather than describe the relationship between local diversity and productivity, diversity-productivity experiments conducted to date appear to better address the relationship between local productivity and the species pool diversity. Nearly all diversity-productivity studies have constructed diversity

treatments using seeded diversity, and several do not report measurements of "realized" diversity (e.g., Naeem et al. 1994, Naeem et al. 1995, Naeem et al. 1996, Tilman et al. 1997b, Symstad et al. 1998, van der Heijden et al. 1998, Hector et al. 1999). This is partially because most of these studies were conducted over short durations (Naeem et al. 1996, 2 months; Symstad et al. 1998, 4 months; Naeem et al. 1994, 206 days) and a "final" diversity measurement may not have indicated equilibrium species diversity (nor does it in the experiments in Chapters 3 and 4). In this context, "species richness" in these experiments closely resembled a seed influx from a species pool, from which the local environment and biota "sampled" to achieve a realized diversity level. (In several experiments, however, species composition was artificially constrained by weeding, e.g., Tilman et al. 1996, Hooper 1998). To explore the relationship between local diversity and productivity, one would first have to construct different levels of realized diversity—that is, levels reasonably stable over the life span of the component species.

Given the important natural role for the sampling effect via species pool diversity and local filtering processes, how can this be best reflected in the design of artificial experiments? First, experimental treatments of seeded species diversity should be viewed as treatments of varied species pool sizes. The most diverse treatments represent the case where all species are available to colonize a site, and the most species-poor plots represent the most depauperate species pools. By monitoring species composition through the course of the experiment, it can then be determined to what extent the local environment and biota select from the

immigrants, and to what extent competitive or facilitative relationships among species affect realized composition. This local assembly process will influence species composition, local diversity, and plot productivity. Second, although experiments at small spatial scales may best reflect scales at which assembly processes in nature are more stochastic than deterministic, this may be trivial because species composition at these scales is often unstable at the scale of a year or more. Moreoever, composition may strongly vary with different rates of propagule supply (e.g., via mass effects; Schmida and Ellner 1984) and experiments should be performed that compare single seed additions with a constant rate of seed addition. Finally, the strong interaction between local biotic and environmental controls of ecosystem productivity suggests that there is a compelling need to perform diversity experiments among a range of environmental conditions both among and within plots.

Separating the sampling effect and other mechanisms: the use and misuse of overyielding

Because the influence of the sampling effect on ecosystem productivity is sensitive to ecological context, it is necessary to separate its effect from the biological interactions of a realized diversity level. Such interactions may be grouped as either those complementary or facilitative, and their net effect quantified as "overyielding." In general, if a plant mixture performs better than its monocultures, it overyields, but there is confusion over which quantities to compare in its calculation. For example, one might compare the absolute yields

of mixtures and monocultures, and define overyielding as either: 1) the event where a crop mixture produces greater yields per unit area than the average yield of its component monocultures (Tilman 1999a); or 2) the event where a crop mixture outperforms its most productive component monoculture per unit area (Garnier et al. 1997, Hector 1998, Hector et al. 1999), also referred to as "transgressive yielding" (Trenbath 1974). The distinction between these two types of overyielding is illustrated in Figure 3. In addition, one might instead compare "relative yields" by dividing a species yield in mixture by its monoculture yield, either at equal total densities (as in a replacement series; de Wit 1960) or equal specific densities among richness treatments (as in an additive design; Harper 1977). The sum of relative yields for all species in mixture is an indicator of complementarity and facilitation (e.g., values over unity in replacement series designs; Vandermeer 1989). Because the quantification of overyielding is crucial to mechanistically explore the influence of species diversity on productivity, the most appropriate operational definition of overyielding must be resolved.

Any investigation of overyielding must first state the goal of the analysis, because different hypotheses are tested depending upon which yield values are compared among treatments. For example, from a farmer's perspective, it may be most profitable to compare the absolute yields of all crop treatments, and statistically determine the assemblage with the highest total yield per unit area. In this case, transgressive overyielding appears the best candidate for measuring yield advantage—unless a mixture yields transgressively, an "all-knowing"

manager could maximize productivity with the most productive monoculture (Tilman et al. 1997a). Indeed, several researchers have argued that transgressive overyielding is the most appropriate indicator of enhanced productivity in more diverse assemblages (Garnier et al. 1997, Loreau 1998b, Huston et al. 2000), and it is obvious that if a mixture yields more than the most productive monoculture, a mechanism other than simply including the most productive species must be operating.

In diversity-productivity experiments, however, it is important to identify the mechanisms by which diversity may influence productivity, and there are several reasons why comparison of absolute yields among treatments, as performed in the calculation of transgressive overyielding, is not the most accurate method for exploring mechanisms of a putative diversity effect. Indeed, it is well-appreciated by agronomists that although there are myriad ways to compare yields in mixture experiments, relative yields, and particularly use of the Relative Yield Total (RYT; equivalently, the Land Equivalent Ratio), are the most robust estimators of overyielding mechanisms (Trenbath 1976, 1978, de Wit 1960, de Wit and van den Bergh 1965), although even RYT is not without its problems (e.g., allelopathy; Trenbath 1976, Loreau 1998b).

One major problem with using absolute yields to quantify overyielding is that the difference between non-transgressive and transgressive overyielding can be caused entirely by the size difference between species, independent of the degree of complementary resource use (or facilitative interaction). This point is illustrated in Table 1 by comparing two scenarios in which the level of niche

complementarity between two species is held constant and only the mature size difference is altered. In both scenarios, species A attains 10% greater biomass per individual in mixture compared to monoculture because it can exploit, for example, additional organic nitrogen in the soil. Individuals of species B, however, attain the same biomass in mixtures as in monocultures. In Scenario 1, individuals of species A have an average monoculture size of 100 g; individuals of species B, 50g. Because A and B are slightly complementary in their use of soil N, species A overyields in mixture and the RYT of the mixture is above unity (1.05) (Vandermeer 1989). The mixture yield, however, is only slightly above the average yield of the two component monocultures (800g compared to 750g)—far from the transgressive boundary of 1000g. In Scenario 2, however, the level of complementarity is the same but the monoculture average sizes of the species are similar: 100g and 95g for A and B, respectively. In this case, though the complementary use of resources is the same (the RYT is still 1.05), the mixture yields transgressively (1025g). Thus, the difference between transgressive and non-transgressive overyielding may be due entirely to the size disparity of component species, not the degree of complementary resource use or facilitative interaction.

Instead, to best estimate complementarity or facilitation and remove the influence of certain species asserting dominance in mixtures, one must show that the enhanced response of one species in mixture is not compensated for by a proportional decrease in another. This indicates that additional resources used by one species in mixture are not completely denied to others (Trenbath 1974). This

can happen by means of resource partitioning (complementarity) or supply of new resources by neighboring species (facilitation). Such non-compensatory responses are obscured when comparing absolute yields among diversity treatments, but are exposed with the use of relative yields (such as RYT), which were designed for the purpose of robustly estimating complementary and facilitative species interactions (de Wit and van den Bergh 1965, Vandermeer 1989).

Another potential hazard in the assessment of relationships between species diversity and mechanisms that cause overyielding is inevitable sampling effects for certain species or combinations that are complementary or facilitative. More diverse mixtures make the inclusion of such species or combinations more probable, and the resulting productivity increase is not the result of a particular realized diversity level but rather the presence of one or a few species from the initial species pool. The problem is especially troublesome because overyielding metrics will (correctly) indicate the occurrence of complementarity or facilitation in assemblages containing the special facilitator or complementary pair but not necessarily be able to identify its cause. The few diversity studies that have quantified overyielding have apparently not appreciated the significance of this problem—again consider the analysis of Hector et al. 1999 where the significant effect of functional richness was likely a sampling effect for legume inclusion. The problem could be corrected by a technique similar to that of single-species relative yields; instead of comparing single-species yields among diversity treatments, the mixture yields could be compared to specific biculture yields.

However, this would require growing plots of all possible bicultures, which may be impossible in experiments of high diversity (e.g., 190 unique biculture assemblages in an experiment of 20 species), and does not account for the role of special facilitators whose effect may not be species-specific. In these cases, it would be advantageous for the most diverse mixtures to include all species except one, including replicates for all one-species removals.

More recently, another metric for calculating overyielding has been suggested by Loreau and Hector (2001) and is likely to become a popular method in biodiversity experiments. Its calculation is closely related to RYT but differs slightly in incorporating the average monoculture yield:

Complementarity effect (CE) = N * avg(M) * avg(ΔRY)

where N is the number of species in mixture, avg(M) is the average monoculture yield of the species in mixture, and ΔRY is the difference between the expected relative yield of a species in mixture (monoculture yield * proportion sown in mixture) and its observed relative yield (mixture yield / monoculture yield). Note that CE/avg(M) -1 = RYT, and all the disadvantages that apply to RYT also apply to CE (Loreau and Hector 2001). In addition, CE has the disadvantage of being sensitive to monoculture yields, and monoculture yields are, in turn, sensitive to changes in environmental conditions. It can therefore be difficult to compare the CE values of mixtures in different environments, a constraint that does not apply to RYT. Chapter 4 contains a detailed analysis of the procedures required to compared CE values in different environments, which typically require

transformations (square-root, log) and, ultimately, division by avg(M), turning it back into RYT.

In what context does diversity or composition influence ecosystem productivity?

Given the dominant role of environmental factors as regulators of both ecosystem productivity and local diversity, it is surprising that several researchers have suggested the expectation of a single, universal relationship between diversity and productivity, regardless of environmental position (e.g., Hector et al. 1999). The recognition that the nature and intensity of species interactions change with environmental context has a long history in ecology (DeCandolle 1820, cited in Clements et al. 1929). Because these same processes underlie the functional response of ecosystems to varied levels of species diversity, it is reasonable to predict that the influence of diversity on productivity is also sensitive to attributes of the surrounding environment.

A good illustration of the interaction between mechanisms of the diversity effect and local environmental conditions is the hypothesized sensitivity of the magnitude of facilitative plant interactions along gradients of environmental stress. It has been suggested that the outcome of plant interaction is the net result of competitive and facilitative processes, with facilitation most important in more stressful habitats such as deserts and salt marshes (Bertness and Callaway 1994). This suggests that, if facilitative relationships among species are a potential means by which diversity influences productivity, such an influence would be most

apparent in stressful or resource-poor environments, and particularly those of severe water stress (Fowler 1986). Diversity-productivity experiments have generally not been conducted in such environments, and facilitation in stressful habitats as a diversity effect may be more significant than these studies have indicated.

The role of complementarity as a driver of the diversity effect should also be sensitive to local environmental conditions. Because the importance of complementarity is dependent upon the spatial and temporal heterogeneity of resources and other environmental factors (Tilman 1999a), the role of complementarity as a determinant of community structure and function should increase with environmental heterogeneity. For example, spatial resource heterogeneity should promote the ability of different species to partition resources (Tilman 1982), a process often invoked as a mechanism of species coexistence (Tilman 1982, Pacala and Tilman 1994) but similarly used to predict an increase in complementarity with the variance of resource conditions (Tilman et al. 1997a). This assumes heterogeneity exists at the scale of species response (Bell and Lechowicz 1994) and conditions do not lie outside the range of physiological tolerances of component species.

The relevance of the sampling effect as a mechanism of the diversity effect, described above, is dependent upon ecosystem scale and the degree of stochasticity in community assembly processes. Because sampling effect processes are affected by species interactions, certain aspects of SE may also be sensitive to environmental gradients. In particular, the influences of the

performance and habitat sampling effects on ecosystem productivity may change along an environmental gradient, and in opposite directions. Consider the expected differences of species niche distributions along a resource gradient (Austin and Smith 1989) (Figure 4A). All species enjoy high, non-toxic resource levels but relatively few have adapted tolerance to low resource levels ("stress" sensu Grime 1974). Under this scenario, randomly selecting a species that fits the environmental conditions of a plot should only be relevant at the lower end of the resource gradient and the upper end of toxicity. This suggests that the habitat sampling effect becomes a more important component of diversity's role in ecosystem productivity as resource stress increases (Figure 4B). At the stressful ends of the resource gradient, however, species have inherently low growth rates (Lambers et al. 1990), and the importance of selecting a species with higher inherent productivity (the performance sampling effect) should increase with resource levels (in the non-toxic region) (Figure 4B). As apparent in Figure 4B, these two facets of the sampling effect may mirror each other along a resource gradient due to the evolutionary trade-offs associated with stress tolerance versus growth rate and competitive ability (Grime 1977). Because niches should be distributed differently along regulator gradients (regulators being environmental factors that affect plant growth and survival but are not consumed; e.g., temperature, salinity, pH; Austin and Smith 1989), so too should the importance of the sampling effect (Figure 5).

Conclusion: why worry about species diversity and productivity in non-agricultural ecosystems?

Within the context of the diversity-productivity debate, there has been surprisingly little discussion about the relevance of ecosystem productivity as an appropriate management concern. On the one hand, half of the terrestrial biosphere is managed for productivity (Pimentel and Kounang 1998). In these ecosystems, maximizing productivity is of obvious importance; it is necessary to meet the demands of the expanding human population and increase the efficiency of natural resource use by minimizing total land use and providing for long-term resource sustainability. In many of these ecosystems, however, species composition is tightly controlled by managers, and the only mechanism of enhanced productivity that appears to be directly attributable to species diversity, the sampling effect, is precluded by non-random human control of composition. Rather, species combinations that are facilitative and complementary are selected to maximize production levels (Altieri 1999, Swift and Anderson 1993). Thus, in half of all terrestrial ecosystems, the ecosystems in which productivity is of overwhelming importance, diversity may play a negligible role in ecosystem productivity.

In the other half of the terrestrial world exist "natural" ecosystems that are managed (if at all) for species or habitat conservation. Productivity in these areas is typically lower and species diversity higher than in agricultural areas, because agriculture has been most successful in fertile areas and species diversity at the local scale is maximized at relatively low fertility levels (Huston 1993). Indeed,

anthropogenic resource enrichment in historically unproductive habitats is a serious threat to biodiversity (Vitousek et al. 1997). It may be asked, then: To what extent is the maximization of productivity in these habitats desirable? Diversity may indeed play an important role in the regulation of productivity in these habitats, most notably via the sampling effect and the size of species pools, but is productivity in these habitats an appropriate management concern? It may be that where ecosystem productivity is a relevant ecosystem property of applied concern, its dependence on diversity is largely made inoperative by intensive regulation of known, productive species assemblages; and where diversity may influence productivity (via the sampling effect), productivity is of little applied importance.

What then are the appropriate goals of experiments investigating diversity-productivity relationships? To start with, it would be beneficial to acknowledge at the outset of an experiment whether it is meant to inform intensely managed, human-dominated ecosystems or ecosystems in which composition is left to naturally fluctuate. This decision would then determine the most appropriate scales, environmental conditions, and species under which the experiment should be performed. For example, studies to inform agricultural systems can profitably be performed at small spatial and temporal scales (with of course advantages to larger scales), over a narrow range of fertile conditions, and with species most relevant to agriculture. In these studies, it is important to remove the sampling effect and quantify the overyielding of certain assemblages (although the sampling effect may still be important in highly fluctuating environments).

Studies to inform natural systems are best performed at larger spatial and especially temporal scales, with species from a common species pool, and, most importantly, under a range of environmental conditions, incorporating resource heterogeneity both within and among experimental treatments.

It is also important to realize the limitations inherent in small-scale diversity-productivity studies that seriously hinder their ability to extrapolate to ecosystems of natural complexity. Such constraints may lead researchers to wrongly conclude that species diversity does not influence ecosystem productivity (and ecosystem function in general). If this is true, then experiments that employ larger amounts of environmental complexity (e.g., resource heterogeneity, environmental fluctuation) should more aptly demonstrate the relationship between diversity and function and perhaps help resolve the diversity-function debate. Indeed, there is emerging consensus that global environmental change is producing a significant role for biodiversity as a stabilizer of ecosystem processes (Schlapfer et al. 1999, Schwartz et al. 2000), largely because the nature of future environments is, for the most part, unknown (Mitchell and Hulme 1999). Stochasticity in community assembly and species composition is the driver of a diversity effect for static ecosystem properties via the sampling effect, and environmental heterogeneity promotes species complementarity as a diversity effect mechanism. Thus, the importance of biodiversity for the functioning of ecosystems appears closely coupled to environmental unpredictability and complexity, and there remains a great need for researchers to explore these

relationships by incorporating greater levels of environmental complexity in their experiments.

Table 2.1. Illustration of the species size-disparity dependence of transgressive and non-transgressive overyielding. The degree of complementarity is the same in both scenarios.

Scenario 1: species A achieves 10% greater biomass in mixture
monoculture size of A individuals = 100g
monoculture size of B individuals = 50g
constant density of 10 plants per plot in replacement series

A mono	B mono	A poly	B poly	avg(mono)	max(mono)	mixture yield	RYT
1000g	500g	550g	250g	750g	1000g	800g	0.55 + 0.5 = 1.05

Scenario 2: species A achieves 10% greater biomass in mixture
monoculture size of A individuals = 100g
monoculture size of B individuals = 95g
constant density of 10 plants per plot in replacement series

A mono	B mono	A poly	B poly	avg(mono)	max(mono)	mixture yield	RYT
1000g	950g	550g	475g	975g	1000g	1025g	0.55 + 0.5 = 1.05

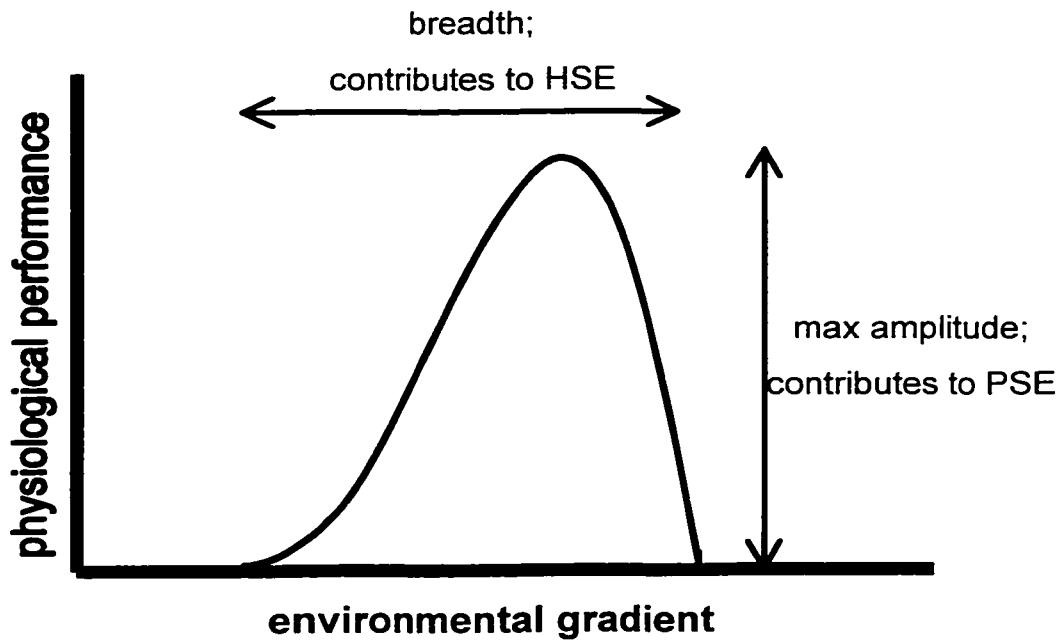

Figure 2.1. Two dimensions of species niche distributions play a role in sampling effects—the habitat SE and performance SE—and their importance is determined by environmental conditions. Species tolerant of low resource levels generally have large niche breadths but small maximum amplitudes; species of fertile habitats have high maximum amplitudes but narrow niche breadths (Smith and Huston 1989).

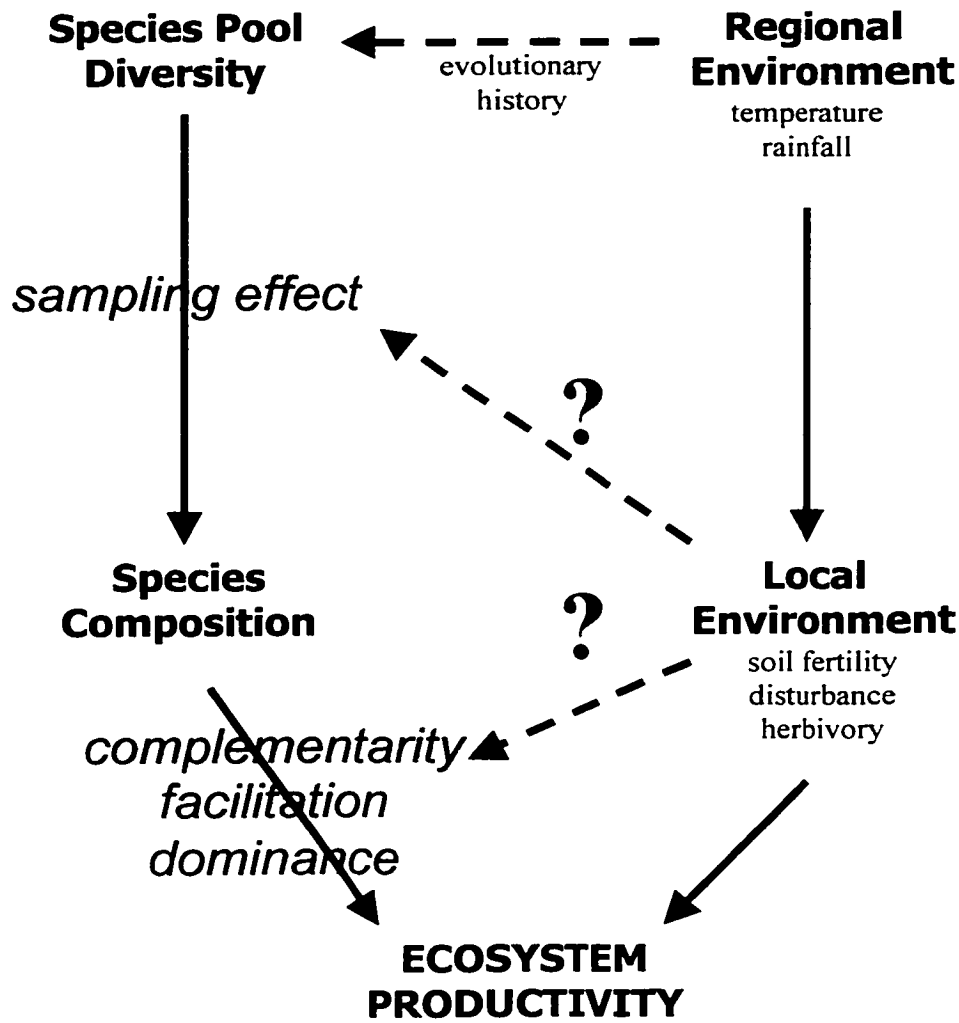

Figure 2.2. Factors that influence ecosystem productivity. Main controls of productivity include regional and local environmental conditions, such as temperature, rainfall, and soil fertility. Species also control ecosystem productivity, and species composition is determined by the diversity and composition of the species pool, which is then "filtered" by the local environment and biota. In this way, species diversity, at least in terms of the species pool, may influence ecosystem productivity (a natural "sampling effect"). Question marks indicate hypothesized relationships only.

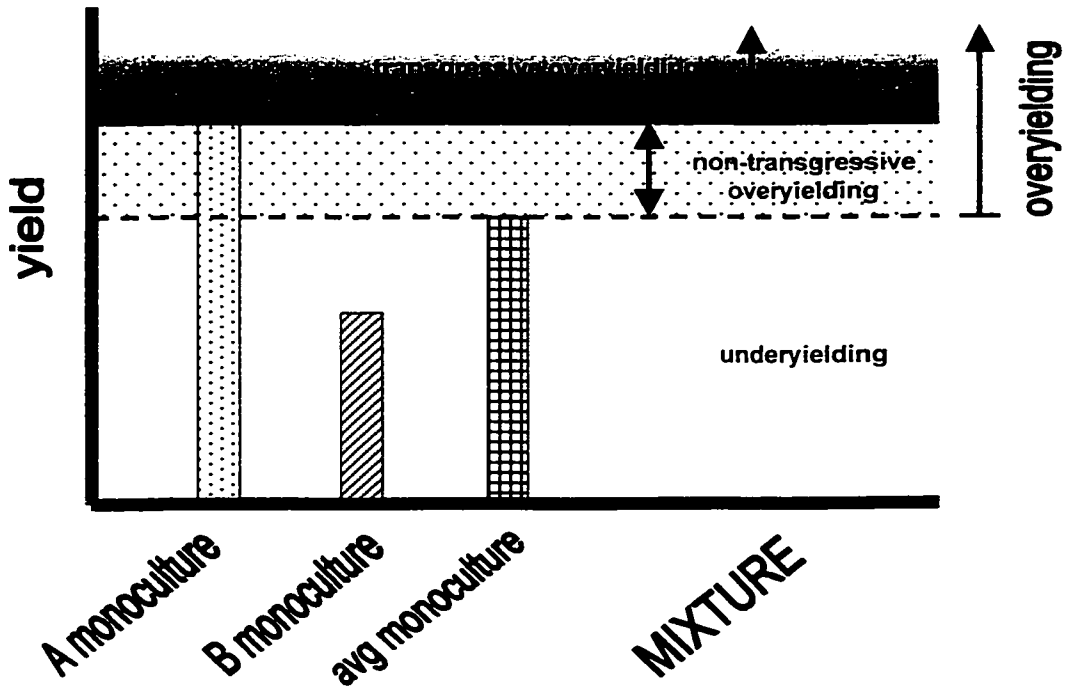

Figure 2.3. Illustration of the two types of overyielding (adapted from Hector 1998). Two monocultures of different total yields are plotted, A and B, and their average yield is indicated. If a mixture of A and B at the same total density yields between the maximum yielding monoculture (in this case A) and the average monoculture yield, it overyields but non-transgressively. If the mixture yield is greater than that of the most productive monoculture, it transgressively overyields (Trenbath 1974). Underyielding is also possible.

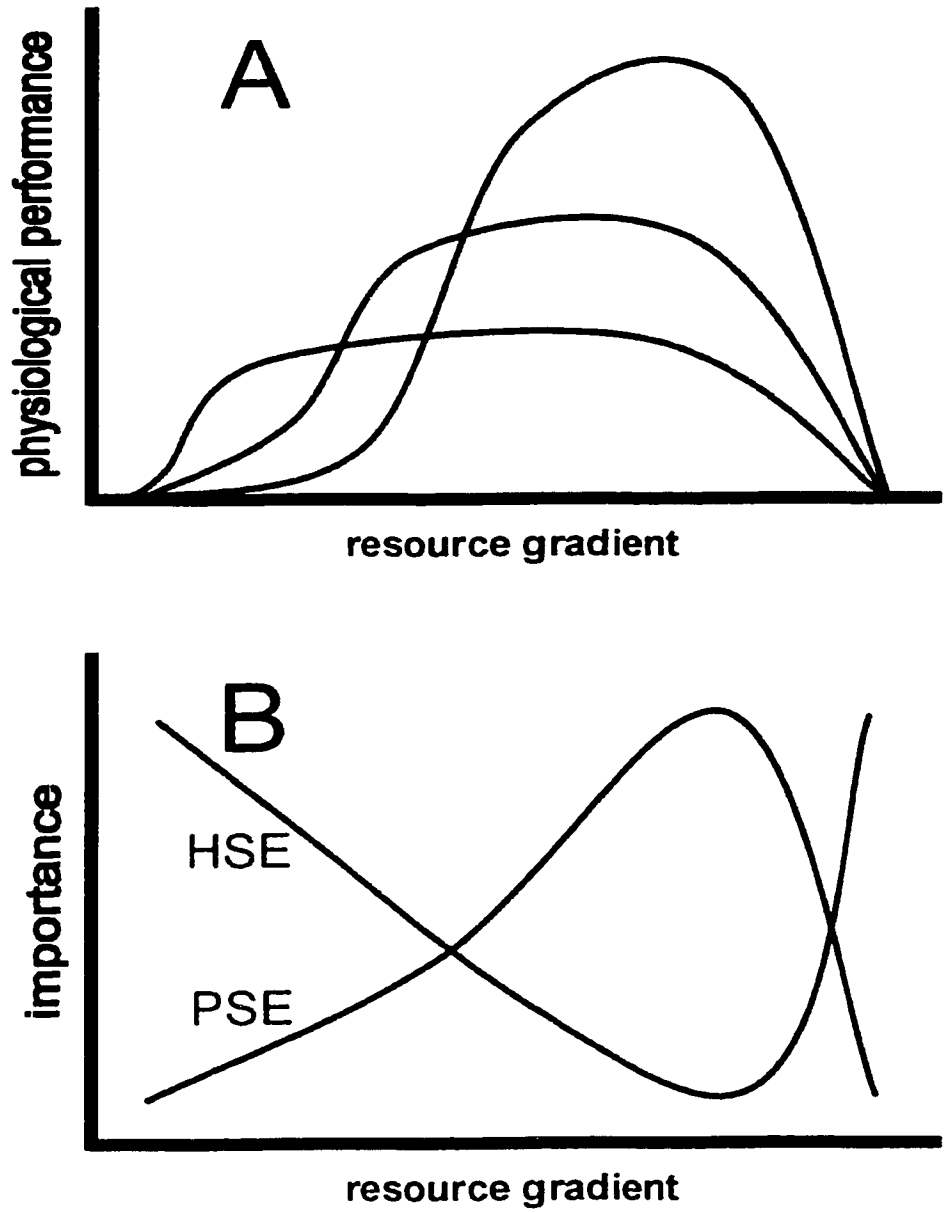

Figure 2.4. **A** Expected niche distributions of species along a resource gradient, adapted from Austin and Smith (1989). **B** Predicted distributions of the importance of the habitat sampling effect (HSE) and the performance sampling effect (PSE) along a resource gradient in randomly-assembled diversity experiments based on the niche distributions of figure A. Note that the two types of sampling effect may mirror each other along the gradient.

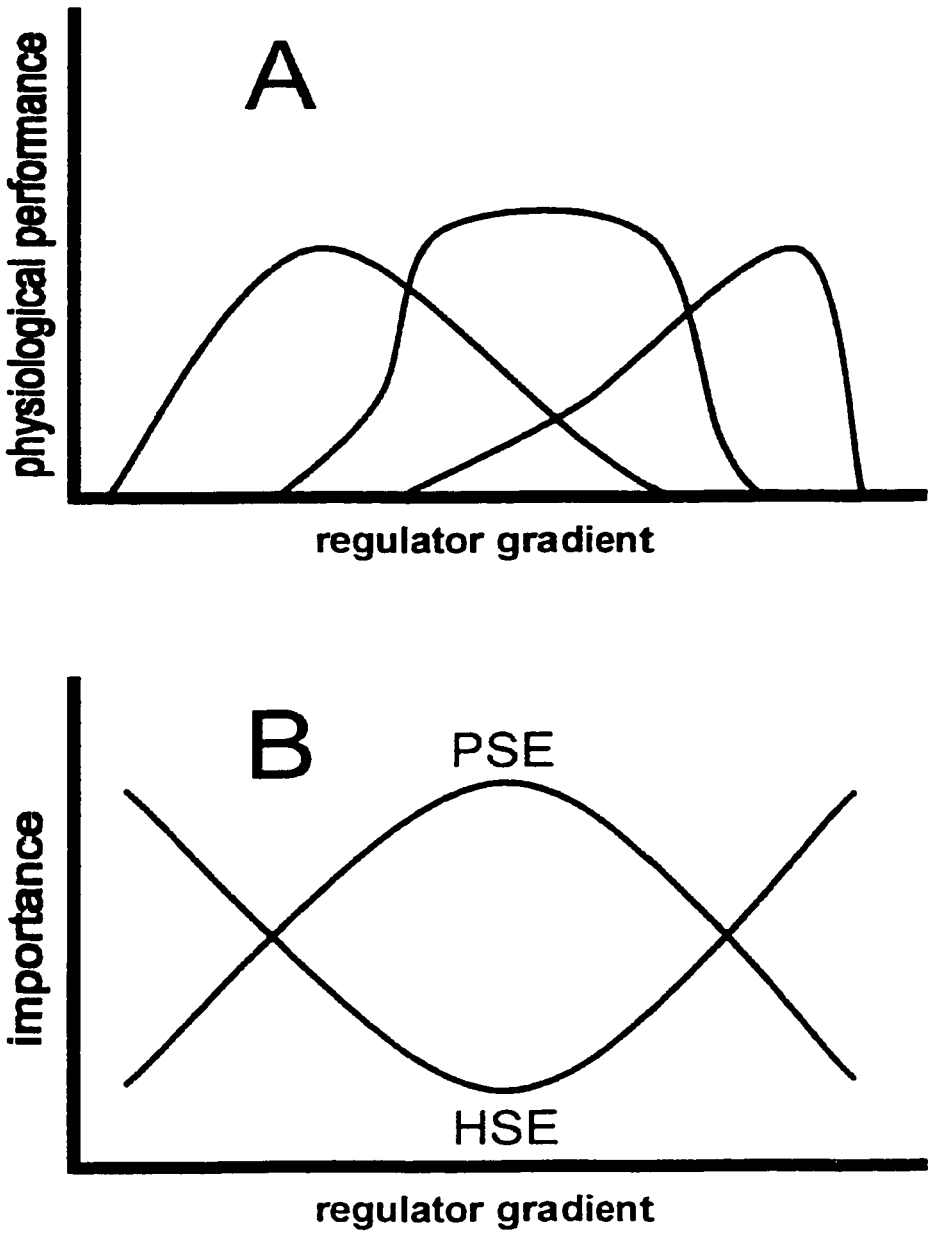

Figure 2.5. **A** Expected niche distributions of species along a regulator gradient, adapted from Austin and Smith (1989) and Huston (1994). **B** Predicted distributions of the importance of the habitat sampling effect (HSE) and the performance sampling effect (PSE) along a regulator gradient in randomly-assembled diversity experiments, based on the niche distributions of figure A. Note that the two types of sampling effect may mirror each other along the gradient.

Chapter 3

Diversity, productivity, and resource availability

Abstract

Experimental evidence that plant species diversity has positive effects on biomass production appears to conflict with correlations of species diversity and standing biomass in natural communities. This may be due to the confounding effects of a third variable, resource availability, which has strong control over both diversity and productivity in natural systems and may conceal any positive effects of diversity on productivity. To test this hypothesis, I independently manipulated resource availability (soil fertility) and sown species diversity in a field experiment and measured their individual and interactive effects on productivity. Although fertility was a far stronger predictor of productivity than diversity, the effect of diversity on productivity significantly increased with fertility. Relative yield analyses indicated that plant mixtures of high fertility treatments significantly "overyielded," or were more productive than expected based on monoculture yields of component species. In contrast, plant mixtures of low fertility treatments had significantly lower-than-expected yields. The effect of diversity on productivity was also driven by sampling effects, where more species-rich mixtures were more likely to include particularly productive species. Unexpectedly, the strength of sampling effects was largely insensitive to fertility

treatment, although the particular species most responsible for sampling effects did change with fertility. These results suggest that positive effects of species diversity on ecosystem productivity in natural systems are likely to be masked by variation in environmental factors among habitats.

Introduction

Plant species diversity has been shown to enhance ecosystem productivity (Naeem et al. 1994, Tilman et al. 1996, Tilman et al. 1997a, Tilman 1999, Hector et al. 1999, Loreau 2000), but the reasons for this remain controversial (Huston 1997, Wardle 1999, Huston et al. 2000, Wardle et al. 2000). One common criticism of experiments that have investigated this relationship is that, in natural systems, plant diversity and productivity (measured as standing plant biomass) either are negatively correlated or show a unimodal pattern in diversity along a productivity gradient (Grime 1973, Huston 1979, Tilman 1982, Grace 1999, Waide et al. 1999). Most experiments in which production has been increased by enhancement of soil resource availability have shown a corresponding decline in species diversity (Kirchner 1977, Goldberg and Miller 1990, Gough et al. 2000). If increased production reduces diversity, can diversity nonetheless increase production? One possibility is that diversity does enhance production, but because factors such as resource availability control both diversity and production in natural systems, the positive effect of diversity on productivity is hidden when compared among ecosystems (Loreau 1998a, Tilman 1999, Loreau 2000).

Studies that manipulate species diversity and resource availability independently could test for this possibility.

There is also disagreement concerning whether mechanisms by which diversity might promote productivity are likely to be similar in experimental and natural systems (Huston 1997, Wardle 1999, Huston et al. 2000, Wardle et al. 2000, Fridley 2001). In experiments where species assemblages are randomly constructed from a fixed species pool, species-rich plots have a higher probability of including those species that have the greatest individual effects on production, a phenomenon called the "sampling effect" (Aarssen 1997, Huston 1997, Tilman et al. 1997a). Determining whether sampling effects might apply in natural ecosystems has been difficult because no experiments have examined the sensitivity of sampling effects to environmental context. For example, sampling effects may be particularly important in environments that promote species dominance, where one or a few species have strong individual control over productivity (Fridley 2001). Resource availability often promotes species dominance in plant communities (Al-Mufti et al. 1977), suggesting that sampling effects should be greater in more fertile habitats. Higher production than expected from the sampling effect ("overyielding" *sensu* de Wit 1960, Trenbath 1974, Joliffe 1998) may be caused by complementary resource use or facilitative interactions among species (Vandermeer 1989, Tilman et al. 1997a, Hooper 1998, Hector et al. 1999). However, as for the sampling effect, the overyielding phenomenon is not well understood (Austin et al. 1988, Vandermeer 1989, Garnier et al. 1997, Fridley 2001).

To assess the relative degrees to which resource availability and species diversity influence productivity, whether these two factors interact, and whether resource availability alters the mechanisms by which diversity influences productivity, I performed a field experiment in which species diversity and resource availability were independently manipulated. I used a soil fertility gradient to manipulate resource availability and constructed plant communities of different levels of sown species richness and composition within these soil treatments. Specifically, my goals were to 1) test whether diversity directly enhances productivity by experimentally controlling resource availability; 2) determine the relative contribution of the sampling effect in enhancing production and the extent to which its role is affected by fertility; and 3) determine whether fertility influences the degree to which plant mixtures overyield.

Methods

I constructed 360 raised-bed plots (50 x 50 cm, 15 cm deep) in an old field at Mason Farm Biological Reserve, North Carolina Botanical Garden, Chapel Hill, NC, USA. Plots were arranged in three replicate blocks. Within size and climate restrictions, I chose a taxonomically diverse group of species with well-known growth characteristics (Table 1). These 10 species were grown in 10 compositions at each of three diversity levels (the 10 possible monocultures, 10 selected two-species "bicultures", and the 10 possible nine-species "polycultures"). The 10 selected biculture compositions were chosen to provide a range of differences in species sizes and to ensure each species was represented in

two unique compositions (Table 1). All 30 species compositions were grown at three fertility levels in each block, with all treatments arranged randomly within blocks. To examine the effect of monoculture density on overyielding analyses, each monoculture was also grown at half density at each fertility level in each of the replicate blocks.

Each plot was filled with a 1:1 mixture of sand and topsoil on top of porous black plastic, and plots of intermediate soil fertility were not further manipulated. Soil of high fertility plots was enriched with 125g "Osmocote" slow-release fertilizer (6-month NPK; The Scotts Co., Marysville, OH, USA), equivalent to 90g N, 30g P, and 60g K/m^2. I supplemented plots of low soil fertility with a 1:1 mixture of hardwood sawdust and table sugar, equivalent to 1.5kg C/m^2. Soil additions for high and low fertility plots were performed on May 31. In addition to reducing nutrient availability to plants, carbon supplementation may alter plant-microbe interactions and other soil processes (Schlesinger 1997); in this study, carbon addition strongly reduced biomass production but soil processes were not investigated.

I established experimental plant communities of different composition and diversity by sowing seed at two different times during the growing season. Total live seed mass rather than seed number was held constant at 4 g (2 g per seed addition) among plots to account for the differences in recruitment success among species of various seed sizes. Live seed mass was calculated by dividing desired live mass by the germination rate of the species (for monocultures), or by dividing the total live mass by 2 (for bicultures) or 9 (for polycultures) and then dividing

this value by each species' germination rate. Initial planting dates among eight of the 10 species were spread over several weeks so that species would germinate at approximately the same time (Table 1). On July 8, *Amaranthus hypochondriacus* and *Avena sativa* were added to their respective plots to replace two species that failed germination and the second seed addition for the remaining eight species was performed. Seed of each species (except *A. hypochondriacus* and *A. sativa*) was added in two cohorts to generate more realistic communities of neighbors of different growth stages.

Plots were weeded weekly and watered daily with an automatic sprinkler irrigation system. *Borago officinalis*, having gone to seed and senesced, was harvested from all plots on August 2. *Festuca ovina* performed poorly and could not be accurately harvested. All remaining species were harvested August 17-19 after all except *Hypericum perforatum* and *Satureja hortensis* had gone to seed. All aboveground biomass was dried to constant mass and each harvested individual plant was weighed to the nearest tenth gram.

I used Type I SS fixed-effect ANOVA models to test square-root transformed total aboveground biomass against the main effects of fertility and diversity, their interaction, and the presence or absence of particular species. Several biomass values were excluded from these analyses, including all *F. ovina* monoculture values (not harvested) and six bare plots, leaving a total dataset of 336 plots. Monoculture density had no effect on monoculture production (Wilcoxon test, $p>0.15$, $n_1=78$, $n_2=81$), probably because the half density treatment was sufficient to maximize yield, so I pooled values from monoculture

density treatments. Note that because diversity and species composition are highly correlated in this experimental design (i.e., the diversity of a given plot is perfectly described by the presence or absence of all species), a comparison of "diversity" effects versus "composition" effects had to be performed using separate models. A first model included only the effects of block, fertility, diversity, and the diversity-fertility interaction (Table 2A). A second model included block, fertility, dummy variables describing the presence or absence of the six species that significantly influenced productivity when included alone in separate ANOVAs, and a diversity term listed last to assess whether diversity could explain any residual variation (Table 2B). Finally, I listed each composition-related variable first in a Type I SS ANOVA to obtain the most liberal estimates for each factor's magnitude of effect, or total sum of squares of the biomass response variable attributed to each factor (Welden and Slauson 1986).

I used two different metrics to estimate overyielding. Relative yields were defined as a species' biomass in mixed culture (biculture or polyculture) divided by its monoculture biomass for the same block and fertility level (de Wit 1960, Hector 1998). Relative yield totals (RYT) were the summed relative yields for all species in a particular mixture. D_{max} was defined as: (total biomass of mixed culture – monoculture biomass of its component species with the largest monoculture value) / monoculture biomass of component species with largest monoculture value (Loreau 1998b, Hector et al. 1999). D_{max} is a more stringent test than RYT for the detection of overyielding, but RYT is a better descriptor of

the mechanisms underlying overyielding, and caution must be used in the interpretation of both metrics (Garnier et al. 1997, Loreau 1998b, Fridley 2001). I square-root transformed RYT and D_{max} values for fixed-effect ANOVAs to achieve normal residual distributions, and zero values (due to bare plots) and several spuriously high values (>5) were excluded.

I also measured the role of sampling effects among fertility levels in two ways. To compare total sampling effects among fertility levels, I used the "selection effect" metric of the "additive partition of biodiversity effects" technique of Loreau and Hector (2001). This estimates a sampling effect for each plant mixture by calculating the covariance between species' monoculture yields and their deviance from expected relative yields in mixture (based on their planted proportions), multiplied by the total number of species in mixture. If species of higher-than-average monoculture values dominate a mixture, the associated selection effect is positive; dominance by smaller, less productive species leads to negative selection effect values. Selection effects were square-root transformed within fertility levels to achieve normality (following Loreau and Hector 2001). To determine which species were most responsible for sampling effects at each level of fertility, I calculated the magnitude of effect for each species as dummy variables in separate ANOVAs for each fertility level (Hector et al. 1999).

Results

Soil fertility, sown species diversity, and species composition were all significant predictors of total aboveground biomass (Table 2). When listed alone

in separate ANOVA models, total species composition had the strongest effect on production, explaining 40% of the variation in biomass among plots, followed by soil fertility (27%), the presence of *Linum usitatissimum* (15%), *B. officinalis* (11%), diversity, and four other species (Fig. 1). Diversity only accounted for 9% of the total sum of squares for plot biomass, even when other aspects of species composition were not considered, and was not a significant predictor of production after accounting for the effects of composition (Table 2). In addition, there was a significant interaction between fertility and diversity in the control of production ($p<0.05$): the diversity effect was marginal in plots of low fertility but increased with nutrient availability, as shown by differences in slopes of separate regression lines for each fertility level (Fig. 2). Production was also significantly influenced by blocking treatment, likely due to slightly different flow rates in the irrigation system, the sprinklers of which were grouped by block.

The effect of the presence or absence of particular species on production, a measure of the sampling effect, was large (Fig. 1), and positive "selection" effects were observed at each level of fertility (Fig. 3). Although calculated selection effects were significantly higher in plots of intermediate fertility than those of low fertility, there was no clear evidence that fertility promoted sampling effects across the whole fertility gradient due to the wide variation of the selection effect metric at the highest fertility level (Fig. 3). Moreover, the two species that had the greatest individual effects on production, *L. usitatissimum* and *B. officinalis*, had their peak effects on opposite sides of the fertility gradient (Fig. 4). Thus, although sampling effects did not appear to vary considerably with fertility, the

particular species responsible for positive sampling effects did change with fertility.

As measured by the Relative Yield Total, overyielding in plant mixtures was significantly affected by fertility ($p<0.01$, $n=133$) but not whether the mixture included two or nine species ($p>0.5$). Bicultures and polycultures exhibited significant overyielding at high fertility (Wilcoxon, $\mu>1$, $p<0.05$, $n=43$) and significant underyielding at low fertility ($\mu<1$, $p<0.05$, $n=43$). At intermediate fertility RYT values were not significantly different from unity ($p>0.5$, $n=47$) (Fig. 5). However, a more conservative overyielding estimate by the calculation of D_{max} values did not indicate overyielding, analyzing plant mixtures as a group or within fertility levels (Wilcoxon, $\mu=0$, $p<0.001$, $n=163$), although low fertility D_{max} values were significantly lower than those of medium fertility (Wilcoxon, $p<0.05$).

Discussion

When manipulated independently in a field experiment using artificial plant communities, soil fertility, sown species diversity, and species composition all significantly influenced productivity. Composition and fertility had much larger effects on production than diversity (Fig. 1), which indicates that, although the richness of the potential colonizing species pool can play a role in ecosystem function, its effects are likely to be overwhelmed by site differences and species identity (Loreau 1998a, Loreau 2000, Wardle et al. 2000). The relative importance of these factors could be influenced by experimental design, including

the range of the fertility gradient and the traits of the species chosen. However, the relatively large effects of species identity and environmental factors compared to the substantially smaller effects of species diversity is likely to be generalizable.

On average, sown species diversity had little effect on production in plots of low fertility, but species-rich plots were twice as productive as monoculture plots at high fertility (Fig. 2). Part of this interaction can be explained by the effects of fertility on overyielding, as measured by relative yields (Fig. 5). Why did plant mixtures in high fertility plots overyield? There are two possibilities. The first is that soil fertility promoted complementary resource use among species, allowing the capture of more total resources in mixtures compared to monocultures (Austin et al. 1988, Vandermeer 1989, Hooper 1998). The species used, however, were of similar growth types and life-histories and the plots were small and probably contained little heterogeneity other than a vertical light gradient. Complementary use of any resource other than light was therefore unlikely; light partitioning has been suggested as a mechanism of diversity effects (Naeem et al. 1994) but is it unclear whether this would be promoted by soil fertility.

The other possible explanation is that fertility promoted facilitative interactions among species, such that "nurse plant"-type interactions (Turner et al. 1966) occurred in the most fertile plots. Plot substrates were 50% sand; although watered daily, plants may have been susceptible to water stress, particularly at midday. Seeds were added in two cohorts, such that seedlings of species that

could not establish due to water stress in the first cohort may have been protected by canopy shade if a suitable canopy was established prior to second sowing. Plots of high fertility had such a canopy by the time of second cohort addition, while those of low fertility generally had small plants with no canopy. Indeed, plot biomass, a reasonable estimator of canopy extent, was a strong predictor of relative yield total ($R^2 = 0.72$, unpublished analysis). However, greater canopy extent with added soil nutrients might also lead to greater water stress for understory seedlings due to a higher total rate of plot water consumption, especially in sandy soil (Ewers et al. 2000, Phillips et al. 2001). A more physiological approach is required to fully determine mechanisms responsible for this fertility-overyielding interaction.

A much larger effect of diversity on production occurred by means of sampling effects for particularly influential species, consistent with other similar studies of experimental plant communities (Tilman et al. 1996, Tilman 1997, Huston 1997, Hector et al. 1999, Huston et al. 2000, Leps et al. 2001). However, despite the expectation that sampling effects promoting ecosystem productivity should increase with soil fertility, there was little evidence that this occurred as estimated by the selection effect metric over all three fertility levels (Fig. 3). The explanation of this relative insensitivity of sampling effects to fertility may be that fertility does promote a sampling effect for fast-growing, competitive species, but a different sampling effect for species tolerant of stressful conditions operated in plots of low fertility, exhibited by the reversal of the importance of *B. officinalis* and *L. usitatissimum* along the fertility gradient (Fig. 4). Thus, in addition to the

increasing probability of selecting more competitive species in species-rich assemblages, sampling effects should also include the greater likelihood of selecting species better adapted to particular habitats, such as those of high nutrient stress. These two separate phenomena have been termed the "performance" and "habitat" sampling effects, respectively (Fridley 2001).

Because this experiment included variation of seeded species diversity rather than a manipulation of standing plot diversity, it may offer grounds for reconciling the apparent conflict between the often negative effects of increased production on diversity and the positive average effects of diversity on productivity in randomly-assembled diversity experiments. This paradox may be resolved by recognizing that diversity is being considered at different scales. High local production may reduce local diversity due to competitive dominance, especially for light (Grime 1979, Huston 1979, Tilman 1982, Grace 1999). However, a larger pool of potential colonizing species might represent a larger range of species traits from which local environmental conditions "sample," thereby increasing the probability of establishment of species with large individual effects on local production (Tilman 1999, Fridley 2001). In the first instance local, realized diversity is the result of a competitive filtering of the species pool available to colonize a particular ecosystem (Pärtel et al. 1996); in the latter, the diversity of the species pool itself directly affects local production. In this experiment, diversity treatments modeled variation in species pool diversity, not local diversity (although these measures of diversity were correlated, as they often are in natural systems; Cornell 1999). Seeded diversity

promoted production largely by means of sampling effects for both highly productive species and stress-tolerant species. At the same time, the considerably greater effect of fertility on production in this experiment suggests that local environmental conditions should have much stronger effects on local ecosystem function than the diversity of the species pool.

Although the design of this study was similar to other plant diversity-productivity experiments (e.g., Naeem et al. 1996, Tilman et al. 1996, Symstad et al. 1998, Naeem et al. 1999, Hector et al. 1999), two caveats in extrapolating these results must be emphasized. First, seven of the 10 species of the species pool were annuals; although taxonomically diverse, these ruderals (*sensu* Grime 1973) would not be expected to exhibit the same range of morphological and physiological diversity of a more natural, perennial community. In particular, studies using species of greater functional diversity, conducted within larger plots, and of longer duration would be more likely to generate complementary or facilitative species relationships, especially those based on phenology (Tilman et al. 1997b, Hooper 1998). Indeed, a consortium of researchers using similar experimental communities but over two years and with ambient species pools concluded that sown species diversity had similar effects on production across a wide range of environmental conditions (Hector et al. 1999; but see Huston et al. 2000). (Interestingly, their data also indicate that diversity had no effect on production at their least productive site, consistent with the present study.) Second, if sampling effects for especially productive or stress-adapted species are a primary means by which diversity enhances productivity, species identity and

environmental context will play a large role in generating diversity-productivity relationships. It is therefore particularly important that interactions between local and regional processes in the control of ecosystem function be investigated using a wide range of species pools and environmental gradients.

Table 3.1. Species of the experimental species pool. *Festuca ovina* (FEOV) was not harvested (see methods) and is not listed. Biculture pairings are the two species that co-inhabited bicultures with the listed species. Biculture compositions were chosen to provide a range of differences in species sizes. Species nomenclature follows Kartesz (1994).

Species	abbr.	family	life-history	biculture pairings	first sowing
Achillea millefolium	ACMI	Asteraceae	Perennial herb	HYPE, SAHO	June 2
Amaranthus hypochondriacus	AMHY	Amaranthaceae	Annual herb	AVSA, FEOV	July 8
Avena sativa	AVSA	Poaceae	Annual grass	AMHY, LIUS	July 8
Borago officinalis	BOOF	Boraginaceae	Annual herb	CAOF, HYPE	June 1
Calendula officinalis	CAOF	Asteraceae	Annual herb	BOOF, FAES	June 1
Fagopyrum esculentum	FAES	Polygonaceae	Annual herb	CAOF, SAHO	June 21
Hypericum perforatum	HYPE	Hypericaceae	Perennial herb	ACMI, BOOF	June 9
Linum usitatissimum	LIUS	Linaceae	Annual herb	AVSA, FEOV	June 1
Satureja hortensis	SAHO	Labitae	Annual herb	ACMI, FAES	June 9

Table 3.2. Summary tables for two Type I SS ANOVA models describing treatment effects on total aboveground biomass. Model A includes the effects of fertility, seeded diversity, and the diversity-fertility interaction without considering other aspects of species composition. Model B describes the residual effects of diversity after accounting for the effects of particular species. Species terms are dummy variables that indicate source variation from the presence or absence of that species; only species that were significant predictors of productivity when listed in an ANOVA model by themselves were included.

Model A:

Source of Variation	**df**	**SS**	**MS**	***F***
block	2	341.9	171.0	9.2**
seeded diversity	2	941.6	470.8	25.4***
fertility	2	2765.9	1383.0	74.5***
diversity x fertility	4	231.9	58.0	3.1*
error	325	6034.6	18.6	

Model B:

Source of Variation	**df**	**SS**	**MS**	***F***
block	2	341.9	171.0	11.1***
fertility	2	2805.8	1402.9	90.8***
L. usitatissimum	1	1492.1	1492.1	96.5***
B. officinalis	1	391.3	391.3	25.3***
C. officinalis	1	51.3	51.3	3.3
F. esculentum	1	0.1	0.1	0.0
S. hortensis	1	110.4	110.4	7.1**
A. hypochondriacus	1	79.3	79.3	5.1*
seeded diversity	2	50.4	25.2	1.6
error	323	4993.2	15.5	

Note: Data were square-root transformed.
* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

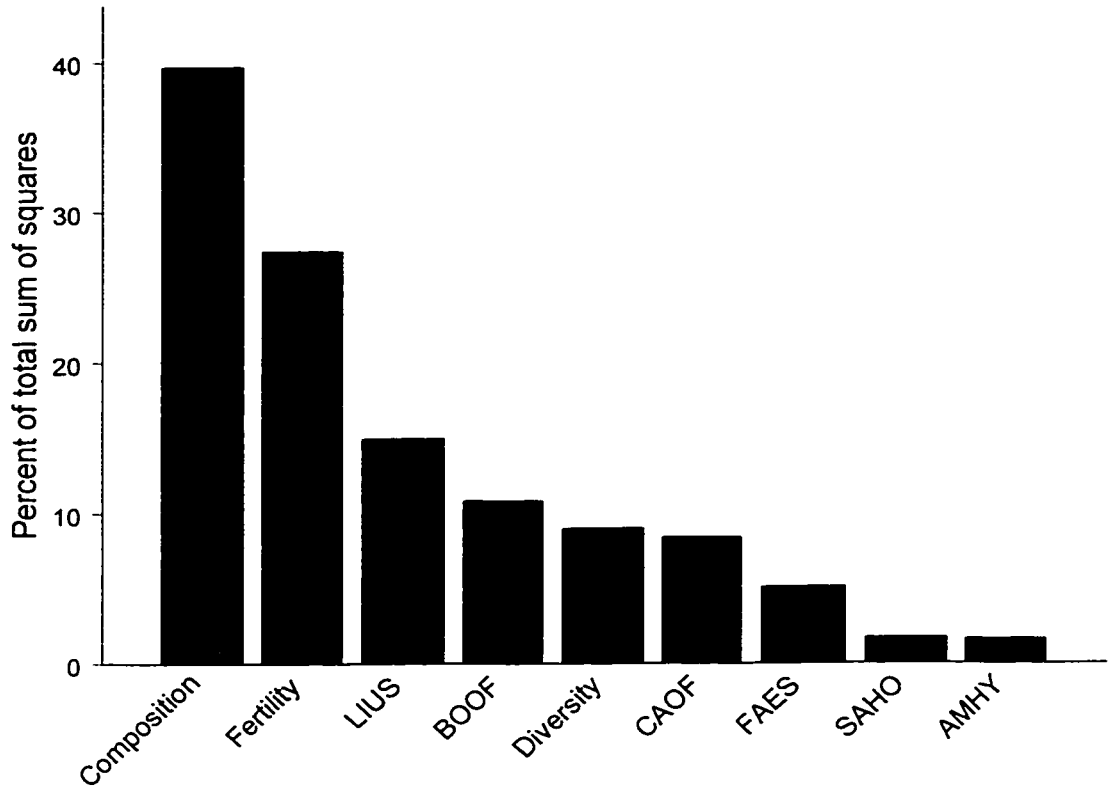

Figure 3.1. Magnitudes of effect for significant factors predicting total aboveground biomass. Species diversity was a significant but weak predictor of productivity compared to fertility, total species composition, and the presence or absence of particular species (species codes listed in Table 1). Bars indicate the associated sum of squares for each factor predicting (square-root transformed) total aboveground biomass when listed individually in a Type I SS ANOVA model.

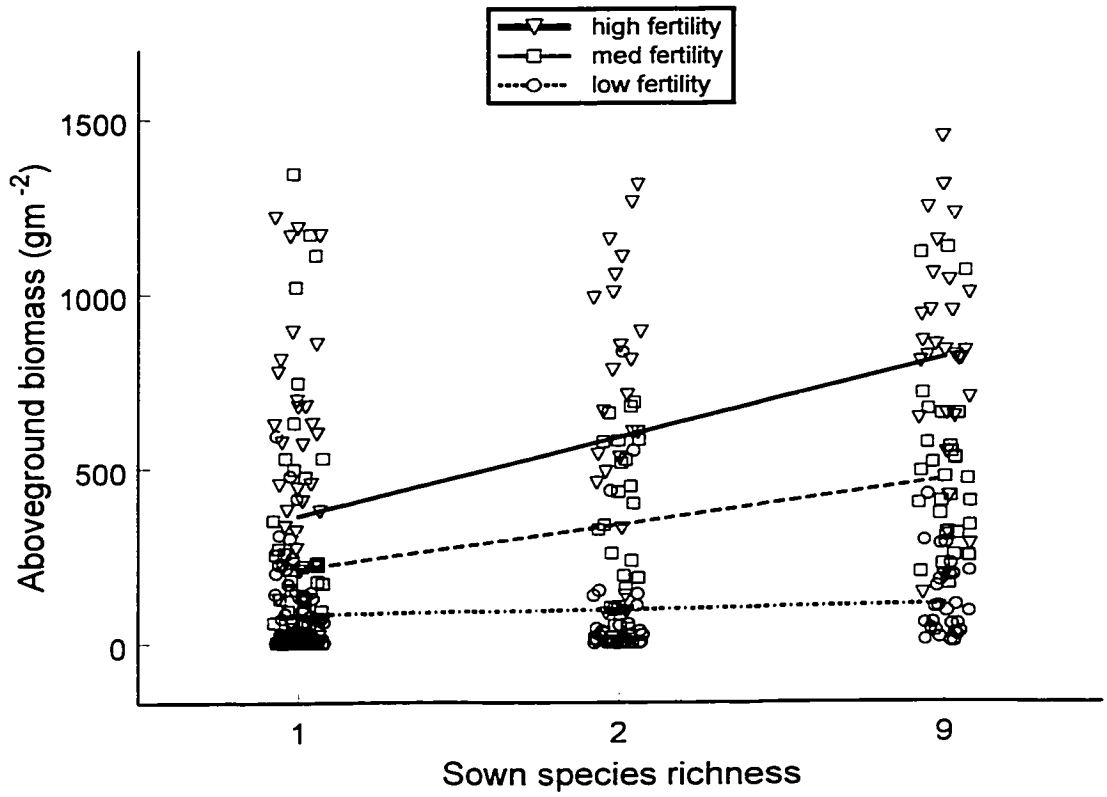

Figure 3.2. The interaction between sown species diversity and soil fertility in the control of total aboveground biomass. The effect of diversity increased with fertility. Linear regression lines are for fertility treatment subsets of plot biomass data. Data values are jittered along the x-axis for clarity.

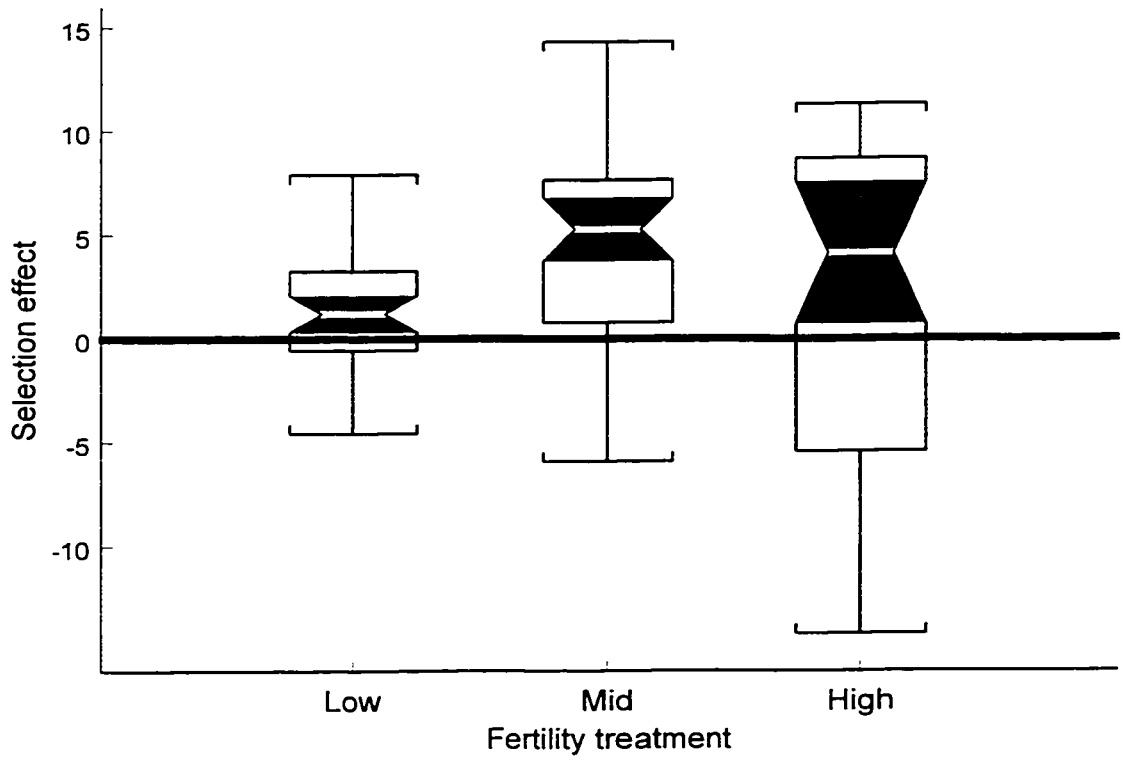

Figure 3.3. Sampling effects in plant mixtures among fertility levels, as calculated by the "selection effect" technique of Loreau and Hector (2001). Positive sampling effects occurred at each fertility level. Box plots indicate the range of the data between brackets, the middle two quartiles within the box, the median value as the white midline, 95% confidence intervals as shaded and notched areas, and extreme outliers as dots. Selection effect values were square-root transformed.

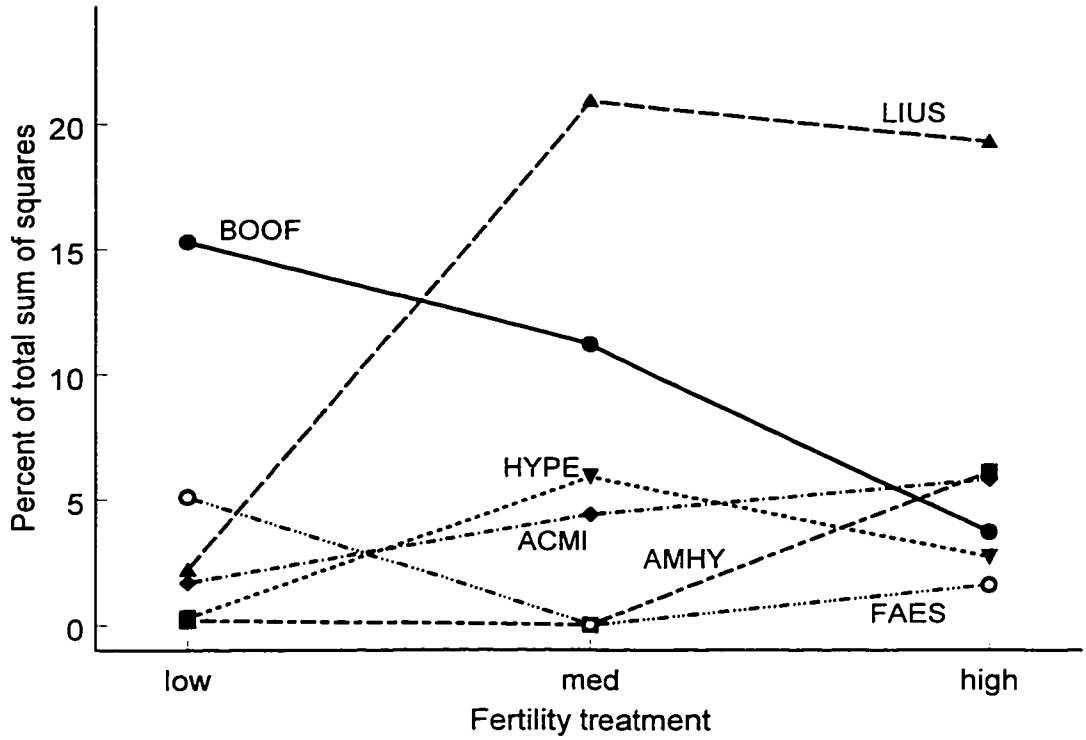

Figure 3.4. Magnitudes of effect for the presence or absence of certain species separated into three fertility treatments. *Borago officinalis* (BOOF) and *Linum usitatissimum* (LIUS) traded-off in importance along the fertility gradient. Percentage of total sum of squares values were derived from ANOVAs of treatment and species effects on biomass performed separately for each fertility level. See Table 1 for species codes.

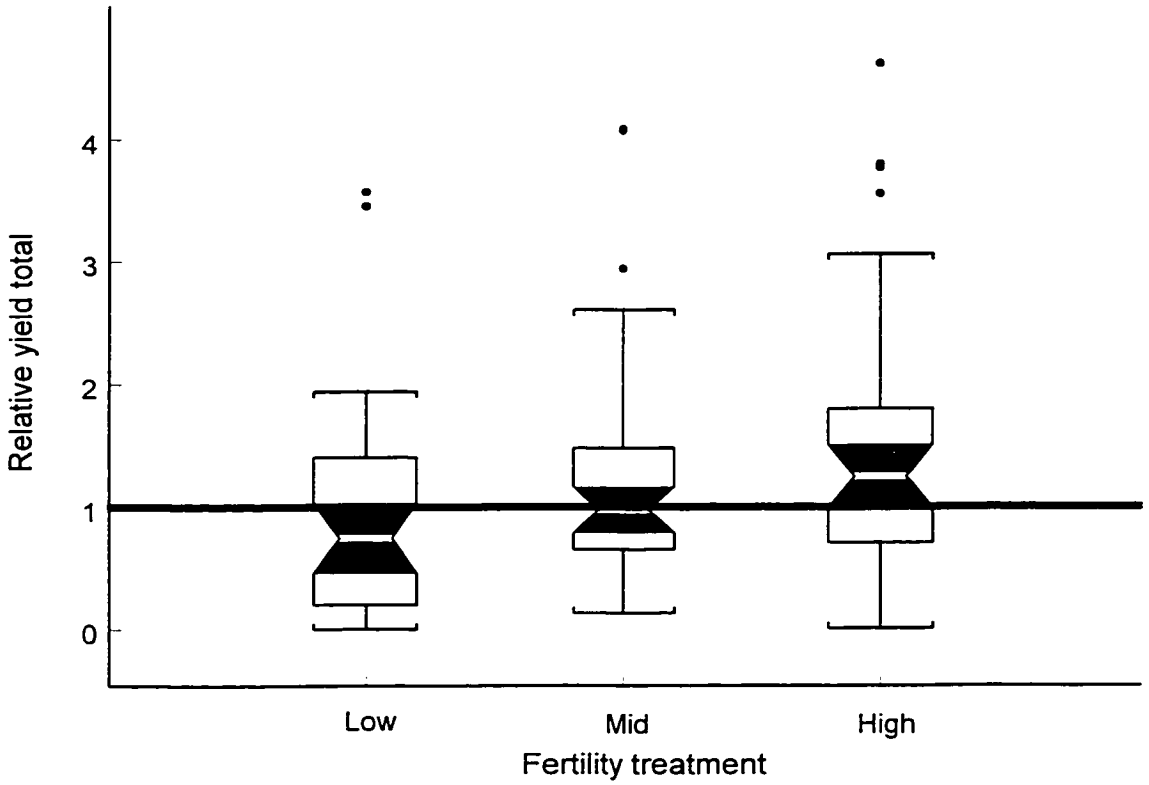

Figure 3.5. Overyielding in plant mixtures among fertility levels, as calculated by the Relative Yield Total. Mixtures of high fertility overyielded; those of low fertility underyielded. Box plots indicate the range of the data between brackets, the middle two quartiles within the box, the median value as the white midline, 95% confidence intervals as shaded and notched areas, and extreme outliers as dots. Overyielding is indicated by RYT values above unity; values below unity constitute underyielding.

Chapter 4

Diversity effects on productivity under different fertility and light conditions

Abstract

Small-scale plant species richness may enhance local productivity if the local environment promotes small-scale resource partitioning (complementary resource use) or causes some species to perform better next to interspecific neighbors (facilitation). Little is known, however, about interactions between species richness and environmental factors such as soil fertility and light levels in the control of ecosystem productivity. To determine whether some environments promote the richness-productivity relationship, I performed a field experiment using plant communities of different levels of species richness and composition, each grown in either high or low soil fertility and either full sun or 50% shade. Species richness significantly enhanced aboveground productivity, and this effect did not depend on environmental treatment. However, overyielding, which measures the net effect of complementarity and facilitation, was significantly enhanced by soil fertility but only in plots of full ambient sunlight. Analyses of relative yields of species of different height and growth habit, coupled with data on the performance of each species in monoculture, support the hypothesis that mixtures overyielded by means of light partitioning (rather than facilitation), an

effect that was precluded by shading and low soil fertility. Overyielding was significantly enhanced by mixture species richness. Competitive dominance by certain highly productive species in mixture, a form of "sampling effect," was also responsible for the effect of richness on productivity, but accounted for less of the total biodiversity effect than complementarity. These results suggest that, at least for mixtures of annual species, small-scale diversity may enhance productivity under certain environmental conditions.

Introduction

There is abundant evidence that small-scale plant species richness over the short term can have positive effects on aboveground production (Naeem et al. 1994, 1995, 1996, 1999, Tilman et al. 1996, 1997b, 2001, Hector et al. 1999). What is less clear is how exactly this effect of diversity operates (Naeem et al. 1994, Huston 1997, Tilman et al. 1997a, Huston et al. 2000, Fridley 2001); whether relatively high small-scale levels of richness are any more productive than just a few species (Vandermeer 1989, Swift and Anderson 1993, Grime 2001); or whether there are particular environments that favor biotic versus environmental control over production (Fridley 2001). One oft-cited mechanism that would allow production to increase with richness is complementary use of resources, such as light partitioning in which differences in growth habit among species allow for greater packing of photosynthetic tissues and thus a more complete harvesting of ambient sunlight (Naeem et al. 1994, 1995). While theoretically attractive, this mechanism has received little direct support and runs

counter to the expectation that a few highly competitive species would usurp the light resource, particularly with regard to perennial herbs (Grime 1977, Al-Mufti et al. 1977, Huston 1979, Goldberg 1990). Nevertheless, a partitioning of the light environment by species of different growth habit is a common principle in the design of intercropping systems (Allen et al. 1976, Vandermeer 1989), and there may be environmental conditions that promote certain forms of light partitioning (Smith and Huston 1989). Soil fertility, for example, may actually promote light partitioning by accentuating growth habit differences among species, particularly with regard to relative canopy heights, as is often the case in stratified forest layers (Halle and Oldeman 1975, Connell and Lowman 1989, Endler 1993, Parker 1995).

In a prior field experiment that examined the small-scale effect of plant species richness on productivity along a soil fertility gradient, complementary resource use, as measured by overyielding metrics, was significantly positive only in the most fertile treatments (described in Chapter 3). The mechanism behind this effect was unclear, which limited the applicability of the experiment to natural and agricultural systems. The uncertainty occurred because the experiment could not distinguish between two potential mechanisms. Because seeds had to successfully establish in a 50% sand soil medium, canopy dominants may have reduced understory thermal and water stresses, facilitating the establishment of seedlings and causing richness to promote productivity in the most fertile plots (where full canopies were present). On the other hand, fertility also promoted differences in growth habit and mature heights among species

(particularly that of the tallest plant, *Fagopyrum esculentum*), which may have in turn enhanced light partitioning. In other words, diversity-fertility interactions in the control of productivity may be due to light (or thermal) relations, but by means either complementarity or facilitative. Explicit manipulation of the light environment may resolve this issue by determining whether certain species perform better in shade (supporting facilitation) or, if not, whether shading precludes overyielding in high fertility plots (supporting light partitioning).

To examine whether fertility enhances diversity effects by promoting light partitioning or facilitative interactions, I performed a field experiment where I grew communities of different richness levels in different soil fertility and light treatments. Soil fertility treatments were performed in a similar manner to a prior experiment to generate the diversity-fertility interaction. If light relations (whether related to partitioning or facilitation) are the cause of diversity-fertility interactions, the overyielding found in high fertility plots should disappear with shading. If facilitation of seedling recruitment by shading is important for some species, they would be expected to perform better in shaded monocultures and their relative yields should be correlated to total overyielding in species mixtures. If light partitioning causes overyielding, there should be no positive effect of shading on monocultures and the relative yields of species in mixture should be better correlated to relative heights and growth habits rather than a species' monoculture response to shading. Therefore, this experiment should be able to determine the mechanism responsible for the diversity-fertility interaction found

in a previous study, and at the same time improve the applicability of these results to agricultural and natural ecosystems.

Methods

Experimental design and construction

Experimental plant communities were created within 252 raised-bed plots (50 x 50 cm, 15 cm deep) constructed for the summer 2000 experiment at Mason Farm Biological Reserve, North Carolina Botanical Garden, Chapel Hill, NC, USA. Plots were arranged in three replicate blocks. Seven taxonomically diverse plant species were chosen from the previous experiment (Table 4.1) because they performed well under ambient growth conditions. These seven species were grown in seven compositions at each of three diversity levels: all seven unique monocultures; seven selected two-species "bicultures"; and all seven possible six-species "polycultures" (Table 4.2). Each of these 21 unique compositions was grown in four different "environments" (21 compositions x 4 environments x 3 replicates = 252 plots). Environments were the four combinations of low and high levels of soil nutrient availability (L and H) crossed with full sun and shade treatments (U and S, respectively). (Henceforth these four environmental treatments will be referred to as LU, HU, LS, and HS.) A split-block design was used with the sun/shade light treatments; each block was divided into halves and one half was shaded. Nutrient treatments were arranged randomly within these light treatments for a block:light:nutrient nesting design.

Each plot was filled with a soil mixture of construction-grade sand (50%) and landscaping topsoil (50%). Soil of high fertility plots was enriched with 125g "Osmocote" slow-release fertilizer (6-month NPK; The Scotts Co., Marysville, OH, USA), equivalent to 90g N, 30g P, and 60g K/m^2. Soil of low fertility plots was supplemented with a mixture of 300 g of hardwood sawdust and 300 g of table sugar, equivalent to a total carbon addition of 1.2 kg C/m^2. All soil additions were performed on May 25. Carbon addition to soils generally reduces nutrient availability to plants but also has many other direct and indirect effects on soil fauna and microbial populations (Schlesinger 1997, Schmidt et al. 1997). For the purposes of this study, C supplementation strongly reduced plant biomass production but other soil processes were not investigated.

Shaded plots were placed under a black air- and water-permeable 50% shade cloth ("Sudden Shade," Dewitt Company, Sikeston, MO, USA). Shade cloths were arranged as one whole sheet per block placed about 2 m above the soil surface, hanging down and fastened to the ground on all sides. Shading treatments were not put in place until June 28, after seedling establishment. Full sun plots were left in the open and separated from shaded plots by at least 2 m. An automated sprinkler irrigation system watered each plot daily and was located beneath shade cloths where necessary. Species not sown into the plots were weeded weekly. All plots were sprayed with the organophosphate pesticide Diazinon every few weeks, beginning June 16, to effectively deter herbivory of *Amaranthus hypochondriacus* by Japanese beetles (*Popillia japonica*). Where

necessary, 1 m-high wire mesh was placed vertically around plot perimeters to keep *Fagopyrum esculentum* from falling into neighboring plots.

Using a seeding technique similar to that of the prior experiment, I established plant communities of different composition and diversity by sowing seed in two cohorts during the growing season. Total live seed mass was held constant among plots at 8 g per seed addition (16 g added total) in a replacement series design to account for differences in recruitment success among species of different seed sizes. Seed added per plot per species was calculated by dividing live plot mass (8 g) by the germination rate of the species (for monocultures), or by dividing the total live mass by 2 (for bicultures) or 6 (for polycultures) and then dividing this value by each species' germination rate. Germination rates were measured by the seed supplier (Johnny's Selected Seeds, Albion, ME, USA) prior to shipment. So that each species would germinate at approximately the same time, species were divided into two groups for initial planting: *Achillea millefolium*, *Borago officinalis*, *Calendula officinalis*, and *Linum usitatissimum* were initially sown on May 30; *A. hypochondriacus*, *F. esculentum*, and *Satureja hortensis* were initially sown on June 8. A second cohort of 8 g live seed of each species was sown on July 9-11 to create more realistic communities of neighbors of different growth stages and also to approximate the experimental conditions of a prior experiment (see Chapter 3).

Plots were harvested August 17-24 after all except *S. hortensis* had set seed. All aboveground biomass was dried to constant mass at 75° C for 48 hours and each species per plot was weighed to the nearest tenth gram.

Data analysis

I used Type I SS ANOVA modeling to determine the significance of main treatment factors (light, nutrients, diversity, composition) and interactions on square-root transformed aboveground biomass. The split-plot design mandated that light treatments be tested against light-within-block error, all other factors and interactions with the within-plot (light treatment) residual error. Two different F contrasts were used to test the significance of species richness treatments (the within-plot residual SS vs. the species composition SS). The ANOVA ordering of light, nutrient, and composition treatments did not affect SS calculations because these factors are perfectly balanced and orthogonal; however, decomposing "composition" into various components required specific factor-ordering hypotheses. Because of this, a separate set of ANOVA contrasts was performed using only the SS for species composition and including the species and diversity terms alone. In this way, the significance of species richness as a determinant of productivity could be assessed against both compositional variation and the full plot residual variation. The use of various treatment and error ANOVA models to test different hypotheses has been strongly encouraged to better interpret diversity-productivity relationships (Schmid et al. 2002). Aboveground biomass data were square-root transformed for all ANOVAs to achieve normally distributed residuals after ANOVA model fitting. All SS calculations were performed with Type I SS; when factor ordering in models affected SS values, I report SS for a specific factor listed first in the model. Type

I SS has been suggested as more informative for comparing magnitudes of fit of factors in diversity-productivity experiments than Type III SS because Type III averages variation among several factors (Schmid et al. 2002, but see also Chapter 3). I also explored the relationship between realized species composition and aboveground biomass in multivariate fashion using nonmetric multidimensional scaling with the PC-ORD software (McCune and Mefford 1999). The ordination reported was created with polycultures only, as a two-axis ordination with the Sorensen distance measure, 5 runs with real data and 20 runs with randomized data (75 maximum iterations).

I examined the mechanisms behind the diversity-productivity relationship in different environments by employing the "additive partition of biodiversity effects" technique of Loreau and Hector (2001). This analysis derives three metrics for each species mixture: a "complementarity effect" (CE), "selection effect" (SE; equivalent and hereafter referred to as sampling effects), and "net biodiversity effect" (BE). CE and SE are calculated separately and sum to BE; each metric may be positive or negative (Figure 4.1). CE is based on the average of the deviation of species' observed and expected relative yields, multiplied by mixture richness and average monoculture yield of the mixture:

$$\textit{Complementarity effect} = N * \text{mean}(M) * \text{mean}(\Delta \text{RY})$$

where N is the number of species in mixture, M is the monoculture yield of the species in mixture for the same block and environment, and ΔRY is the difference between the expected relative yield of a species in mixture (monoculture yield *

proportion sown in mixture) and its observed relative yield (mixture yield / monoculture yield). Positive CE values indicate net overyielding sensu de Wit (1960) (see also Chapter 2), such that species on average perform better in mixture than monoculture (Figure 4.1). CE values less than zero indicate underyielding. Sampling effect values are based on the covariance between monoculture yield and mixture relative yields:

$$\textit{Sampling effect} = N * \text{covariance}(\Delta\text{RY}, M)$$

Positive SE values indicate species of greater monoculture yields dominate mixtures and negative values indicate species of lesser monoculture yields dominate mixtures (Figure 4.1), ignoring "selection" effects associated with species combinations of two or more. BE, the net biodiversity effect, is the difference between the expected mixture yield (based on monoculture yields) and the observed mixture yield, and is the sum of CE and SE. Because good monoculture data are extremely important in relative yield-type analyses (Vandermeer 1989), I replaced three *B. officinalis* values that were extremely low (<1 g) with the mean values of the other two replicates for these treatments to prevent them from spuriously inflating relative yield calculations.

CE, SE, and BE data sets derived from this analysis each contained 168 values from mixtures of bicultures and polycultures and were each independently fitted to Type I SS ANOVA models to determine whether values differed with mixture richness (2 or 6), environmental treatment, and their interaction. Untransformed distributions of these three response variables were not normally

distributed, so I transformed them in two ways. The first was a square-root transform (maintaining negative values) as suggested by Loreau and Hector (2001), which had different degrees of effectiveness for each variable. The additive partition metrics are sensitive to the average monoculture productivities of a particular environmental treatment, which is not necessarily corrected for by a square-root transformation. In response, I divided the values for each metric by their average monoculture value (present in the CE, SE, BE calculations) as "relative" metrics, and these were also square-root transformed in some cases to better achieve normal residual distributions in ANOVA model fitting. In a sense, relativization in this way transforms the CE metric into a Relative Yield Total (note RYT - 1 = CE/mean(M)). A few extreme outliers were removed in CE and SE values (and their relative and square root derivatives), where CE values were greater than 300 (3 values) and SE values were less than –250 (2 values); sample sizes and transformations used are indicated in ANOVA tables for particular tests.

Results

Absolute effects of diversity and environmental treatments on productivity

Soil fertility and species richness strongly enhanced aboveground plot productivity in additive fashion. Although species richness explained about half as much variation in plot productivity as fertility, the effects of species composition were greater than richness even after accounting for richness sums of squares (Table 4.3). Light treatments did not significantly alter productivity, nor were there significant interactions between any of the main effects (light, fertility,

richness; Table 4.3). The statistical model suggests that richness enhanced productivity in the same manner in each environmental treatment, even though the slope of the richness-productivity relationship is slightly greater in full sun treatments (Figure 4.2). The statistical insignificance of light treatment (and the light interaction terms) may be due to the loss in statistical power associated with using light as the "plot" or blocking factor in the split-plot design (Snedecor and Cochran 1967).

Effects of species composition vs. species richness and species identity

The sums of squares attributed to sown species composition can be decomposed into various non-independent components, including initial species richness, the presence or absence of each species, and the total SS accounted for by species identity alone (i.e., no interspecific interactions). Even when contrasted with the total composition SS (instead of the residual SS in Table 4.3), richness significantly enhanced productivity ($p<0.05$), which indicates that the effects of richness operated above and beyond the effects of species composition. Nonetheless, a far greater percentage of composition SS could be explained by species identity, taken as a whole (83% composition SS) or decomposed into the presence or absence of individual species in the initial seed mixture (Figure 4.3). This also means that, at a minimum, 17% of the variation in productivity that was related to species composition must be the result of interspecific interactions of some sort, whether pairwise or of higher order.

The presence or absence of *A. hypochondriacus* could itself explain 62% of the compositional variation in productivity (Figure 4.3), indicating large sampling effects for this species in mixture. NMS ordination separated polyculture composition largely on the basis of *A. hypochondriacus* abundance, which was in turn strongly related to total mixture biomass (Figure 4.4), further attesting to the importance of *A. hypochondriacus* in determining mixture composition and productivity. The performance of *A. hypochondriacus*, in turn, was influenced by environmental treatment, and the shaded, low fertility plots strongly limited monoculture production of this species (Figure 4.5). Polyculture composition as a whole, however, was not clearly related to environmental treatment in the NMS ordination.

Like *A. hypochondriacus*, species in general performed best in full sun and high soil fertility, followed by high fertility and shaded treatments, low fertility full sun plots, and consistently at the bottom were shaded, nutrient-poor plots (Figure 4.5). The major exception was *C. officinalis*, which yielded the highest in nutrient-rich but shaded treatments. *A. millefolium* also slightly preferred shading over full sun in monoculture. *S. hortensis* was apparently dependent upon high levels of both light and nutrients, and in general performed poorly in mixture.

Composition and richness: initial treatments vs. realized values

When fitted as first terms in ANOVA models predicting square-root transformed productivity, both realized diversity and realized composition explained more variation in productivity than initial diversity and composition,

respectively (Table 4.4; compare models A and B, C and D). Also, adding initial diversity and composition to these models as second terms did not significantly explain any more variation in productivity, suggesting that initial composition only served to determine final composition and richness and did not act beyond that.

Additive partition of biodiversity effects

Untransformed complementarity (CE), sampling (SE), and net biodiversity (BE) effects were all significantly greater in mixtures of 6 species than mixtures of 2 species (Figure 4.6). Because net biodiversity effects are the sum of CE and SE for a particular mixture, the effect of richness on BE was especially apparent. When relativized by average monoculture biomass to account for differences in average productivity among treatments, the effects of richness on CE and BE remained but for SE disappeared (Table 4.5). Environmental treatment significantly influenced complementarity, sampling, and net biodiversity effects (Table 4.5, Figure 4.7). Complementarity effects were significantly greater than zero in the high fertility-full sun treatments and were significantly higher than other environmental treatments; CE values in low fertility, shaded plots were marginally significantly positive (Figure 4.7). Sampling effects were significantly positive in only the high fertility-shaded treatments and significantly greater than other environmental treatments (Figure 4.7). Net biodiversity effects were significantly positive in all environmental treatments except low fertility-full sun; in addition, BE values for high fertility, full sun plots were significantly greater

than those for low fertility, shaded plots (Wilcoxon test, n1=n2=42, p=0.01) (Figure 4.7).

Relative yields (mixture mass / monoculture mass) calculated for each species independently were also influenced by environmental treatments for several species and in different patterns (Figure 4.8). *A. millefolium* and *A. hypochondriacus* performed best in mixture in the LS treatment even though neither species performed best in monoculture in that treatment (Figure 4.5). *F. esculentum* performed best in mixture in HS treatment, while *C. officinalis* achieved highest relative yield in the LU treatment, even though its highest monoculture yield occurred in the HS treatment. Relative yields of the shade-loving *C. officinalis* could explain nearly half the variation in CE (when relativized by average monoculture biomass) for all mixtures ($R^2 = 0.47$, $p<0.0001$), but not as much as that of *A. hypochondriacus* ($R^2 = 0.61$). Indeed, *A. hypochondriacus* had consistently one of the highest relative yields over all environments, suggesting that, at least for this species, monoculture yield and mixture success were related, irrespective of environmental treatment.

Dominance, sampling effects, and environment

Plot productivity was unrelated to the percentage of dominance by the dominant species in mixture ($p>0.6$), suggesting that species dominance was not the primary cause of the richness-productivity relationship. Furthermore, although Pielou's dominance metric ($1/J$) was significantly and positively related to SE no matter which transformation of SE was used (all $p<0.05$), the fit of these

variables was very poor ($R^2 = 0.05$), and environmental treatments did not influence dominance (Pielou's, $p>0.1$). In addition, relative abundance rankings of species in polyculture were largely insensitive to environmental treatment, the exception being the low fertility, shaded treatment where *A. hypochondriacus* had a significantly lower relative abundance than in the other three environments, and *C. officinalis* had higher relative abundance than in low fertility, full sun plots. This may be due to strong competitive interactions between these two species, as their relative abundances in polycultures had a high negative covariance.

Discussion

In a field experiment in which I varied local plant species richness and composition within four different environments of different nutrient and light levels, species richness was a significant promoter of productivity across all environments. The effect of richness remained even after accounting for the effect of species composition, suggesting that the effect of richness was above and beyond the inevitable differences in species composition among richness treatments.

Small-scale species richness promoted productivity by two principal means. The higher probability of including the highly productive and competitive *A. hypochondriacus* in more diverse plots significantly promoted productivity across all environments, which was the main reason that species identity could explain over 80% of the variation in productivity attributed to species composition. The remaining variation, however, must be attributed to species

interactions, suggesting that some form of overyielding significantly enhanced productivity even at this small-scale. Indeed, overyielding was significantly higher in polycultures than bicultures, leading to higher net biodiversity effects as local species richness increased.

As measured by the complementarity effect, overyielding was promoted by high fertility, consistent with the results of a previous field experiment in which sown species richness and nutrient availability were independently manipulated (Chapter 3). As predicted, this phenomenon disappeared when these plots were put under 50% shade (discussed below). Surprisingly, sampling effects were significantly higher in these high fertility, shaded plots than the other three environmental treatments (Figure 4.7); this may have been due to the coupled high relative yields of *A. hypochondriacus* and *F. esculentum*, species with two of the highest monoculture values.

The additive partition technique suffers from the same limitations as those of relative yield-type calculations (Huston et al. 2000, Loreau and Hector 2001). For example, evidence of complementary resource use (or facilitation) is determined by positive average deviations from expected yields across all mixture species, rather than a "transgressive overyielding" approach where complementarity is indicated by higher mixture yields than those of the most productive monoculture (Garnier et al. 1997, Loreau 1998, Spaekova and Leps 2001). Transgressive overyielding is a more conservative estimate of complementary resource use, and in this study the most productive assemblages were bicultures in full sun and monocultures in shade (Figure 4.2). Thus,

although 6-species mixtures were *on average* more productive than 2-species mixtures, any particular transition from mixtures of 6 species to 2 species may not be accompanied by lower productivity. However, even the transgressive approach to complementarity is not foolproof, as relative species sizes can obscure true complementary relationships with this approach (Fridley 2001).

Facilitation vs. light partitioning

Species in mixture performed better than expected based on monoculture performance, or overyielded, only in the high fertility, full sun plots, as measured by the complementarity effect. Overyielding may be caused by either complementary resource use among species in mixture or facilitative interactions among species (Fridley 2001; see Chapter 2). In this experiment, complementary resource use was unlikely for any resource other than light because the plots were relatively small and exhibited little soil heterogeneity. Facilitation of seedling recruitment of species intolerant to the relatively dry and hot conditions of the 50% sand substrate may have operated in plots where intact canopies were available from neighboring species at the same time the second seed cohort was establishing; such canopy availability would have been promoted by fertility (Chapter 3). In much the same way, fertility may have promoted light partitioning by accentuating the size differences among species. When high fertility plots were shaded, overyielding effects disappeared—was this because the vertical light gradient was reduced, precluding light partitioning, or because

certain species were not facilitated because they performed better in monoculture under shade?

The evidence suggests against facilitation. Only two species performed better in monoculture in shade: *A. millefolium* and *C. officinalis* (Figure 4.5). Of these, *C. officinalis*' benefit from shade was greater and *C. officinalis* performed much better in most mixtures (Figure 4.8). Relative yields of *C. officinalis* could explain nearly half the variation in complementarity effect, but not as much as that of *A. hypochondriacus*. Furthermore, although the only significant positive correlation of relative yields was between *C. officinalis* and *B. officinalis*, *C. officinalis* performed just as well with *F. esculentum* as *B. officinalis* in biculture, and the relative yields of *C. officinalis* and *F. esculentum* were not correlated. If *C. officinalis* was responsible for the overyielding effect in the HU treatment, the fit of *C. officinalis* relative yield and complementarity effect should be greater in those plots than when those plots were shaded; in fact, the fit was worse in the HU treatment. Finally, polycultures not containing *C. officinalis* should have exhibited some of the lowest complementarity values if facilitation for *C. officinalis* was significant, but these polycultures had relatively high complementarity values, even in the HU treatment.

The evidence for light partitioning in the HU treatment is more compelling, following the predictions of Naeem et al. (1994, 1995) that small-scale diversity may promote production by allowing a greater packing of photosynthetic tissues. The light partitioning hypothesis can work only if the species in the lower height strata—the species partitioning light—respond best to

the full sun gradient; canopy species are presumably competing largely with themselves and should therefore only respond to different intraspecific density levels. As plots are shaded, the vertical light gradient is diminished and understory species should perform relatively worse in mixture. The data support this scenario. Approximate relative heights of the seven species in mixture are:

FAES > LIUS > AMHY > BOOF > CAOF > SAHO > ACMI

Light partitioning may have occurred in the high fertility, full sun plots if species in the understory (i.e., below *F. esculentum*) account for changes in relative yields between HU and HS treatments. Indeed, the relative yield of *F. esculentum* was markedly reduced in the HU treatment compared to under shade, while the relative yields of all species below *F. esculentum* (except *S. hortensis*, which performed poorly in mixture everywhere) increased markedly in full sun (Table 4.6). Thus, available evidence strongly suggests that soil fertility promotes light partitioning by accentuating differences in species' heights and growth forms, an effect that shading removes by taking away the full light gradient.

Relevance to natural and agricultural ecosystems

The occurrence of light of partitioning as a mechanism of productivity enhancement by small-scale plant species richness begs the question as to whether this should be expected to occur in highly fertile, natural old-field or grassland plant assemblages. The critical difference between most such natural assemblages and the experimental plant communities is that, while the species richness of high fertility plots was still high at the conclusion of the experiment,

this would be not expected to be stable in most natural systems. Indeed, natural "monocultures" often occur in sites of extremely high soil fertility (Grime 2001). Species that dominate these monocultures, such as *Urtica dioica*, leave little room for light partitioning from other species because they are highly resistant to invasion, likely a result of high competitive ability for light (Grime 1977). Had this experiment been performed instead with perennials and lasted several years, the interaction of complementarity effects with fertility probably would have disappeared due to local species extinction. On the other hand, sampling effects for particularly productive species, in which competitive ability and productivity are positively related, would be expected to become greater over time. But as a general rule the light partitioning mechanism is unlikely to be relevant in species-rich natural plant assemblages as a control of productivity.

On the other hand, these experimental results may have relevance for crop assemblages where "realized" values of species richness are of little concern due to crop harvest at the end of the growing season. Indeed, partitioning the light environment is one of the bases for intercropping designs (Allen et al. 1976, Vandermeer 1989), but there is little known about the interaction of these complementary relationships with environmental factors like soil fertility. This experiment suggests that soil nutrient enrichment, a concomitant benefit of intercropping practices in general (Vandermeer 1989), has a secondary benefit of increasing the intensity of complementary relationships among crop species. Indeed, overyielding in intercropping systems tends to increase as size differences among crop species increase; for example, some of the highest overyielding

values in the intercropping literature are found in agroforestry tree-shrub-forb systems (Ewel 1986). Soil fertility may act in the same way for a particular intercropping assemblage by accentuating the height differences among crops. The interaction of species composition and environment in intercropping studies has apparently received little attention, however, and should become a focus of future studies.

Future directions

The significant interactions of biotic and environmental factors in this experiment and the previous experiment should be a strong mandate to include environmental variation in future biodiversity experiments. Two important points are made when environmental variation is included. The first is that the effects of species richness are always less than the main environmental treatments that control productivity, as was emphasized in the first experiment (Chapter 3). The second is that the effect of species richness tends to change with environmental position. In the first experiment, soil fertility promoted the diversity effect; this was also true in the second experiment but became more complicated when another environmental factor (light) was manipulated independently of fertility. By concomitant manipulations of species composition, richness, and environmental factors, researchers will be able to put the effects of species richness on productivity in their proper context and be able to identify the most likely environmental conditions under which diversity effects will occur.

Table 4.1. Species of the experimental species pool listed in descending order of monoculture yield. Biculture pairings are the two species that co-inhabited bicultures with the listed species. Biculture compositions were chosen to provide a range of differences in species sizes. "Size" is the maximum monoculture yield of species in the full sun and high soil nutrient treatment. Species nomenclature follows Kartesz (1994).

Species	abbr.	family	life-history	biculture pairings	size (g)
Borago officinalis	BOOF	Boraginaceae	Annual herb	CAOF, LIUS	287.5
Amaranthus hypochondriacus	AMHY	Amaranthaceae	Annual herb	ACMI, LIUS	285.7
Fagopyrum esculentum	FAES	Polygonaceae	Annual herb	CAOF, SAHO	215.0
Linum usitatissimum	LIUS	Linaceae	Annual herb	AMHY, BOOF	176.3
Calendula officinalis	CAOF	Asteraceae	Annual herb	BOOF, FAES	166.5
Achillea millefolium	ACMI	Asteraceae	Perennial herb	AMHY, SAHO	150.0
Satureja hortensis	SAHO	Labitae	Annual herb	ACMI, FAES	127.6

Table 4.2. Plant community compositions at each experimental level of species diversity.

Monocultures (7)	Bicultures (7)	Polycultures (7)
ACMI	ACMI + AMHY	AMHY + BOOF + CAOF + FAES + LIUS + SAHO
AMHY	AMHY + LIUS	ACMI + BOOF + CAOF + FAES + LIUS + SAHO
BOOF	BOOF + CAOF	ACMI + AMHY + CAOF + FAES + LIUS + SAHO
CAOF	CAOF + FAES	ACMI + AMHY + BOOF + FAES + LIUS + SAHO
FAES	FAES + SAHO	ACMI + AMHY + BOOF + CAOF + LIUS + SAHO
LIUS	LIUS + BOOF	ACMI + AMHY + BOOF + CAOF + FAES + SAHO
SAHO	SAHO + ACMI	ACMI + AMHY + BOOF + CAOF + FAES + LIUS

Table 4.3. Type I SS ANOVA for main treatment effects and interactions on aboveground productivity. Split-plot design means that the "light" factor is contrasted with the among-light treatment (larger) error; all other F terms represent contrasts with (within-plot) residual error.

Source	df	SS	MS	F	p
block	2	503.3	251.7		
light	1	313.3	313.3	13.2	0.17
fertility	1	754.8	754.8	99.8	**<.001**
richness	2	402.5	201.3	26.6	**<.001**
composition	20	668.0	33.4	4.4	**<.001**
light:fertility	1	0.1	0.1	0.002	0.97
fertility:richness	2	25.3	12.7	1.7	0.19
light:richness	2	20.4	10.2	1.3	0.26
light:fertility:richness	2	14.7	7.4	1.0	0.38
residual	216	1634.0	7.6		

Table 4.4. Four Type I SS ANOVA models evaluating relationships between effects of initial and realized composition and richness on productivity. See text for details.

Model	Source	df	SS	MS	F	p
A	**realized composition**	44	1362.9	31.0	2.2	**<0.001**
	initial composition	12	271.8	22.6	1.6	0.09
	residual	195	2749.2	14.1		
B	**initial composition**	22	1076.7	48.9	3.5	**<0.001**
	realized composition	34	557.9	16.4	1.2	0.26
	residual	195	2749.2	14.1		
C	**realized richness**	1	421.6	421.6	26.5	**<0.001**
	initial richness	2	19.5	9.7	0.6	0.54
	residual	248	3942.7	15.9		
D	**initial richness**	2	402.5	201.3	12.7	**<0.001**
	realized richness	1	38.6	38.6	2.4	0.12
	residual	248	3942.7	15.9		

Table 4.5. Type I SS ANOVA tables for the additive partition metrics (complementarity, sampling, and net biodiversity effects) in response to mixture richness, environmental treatments, and their interaction. "Env treatment" represents the four light-nutrient treatments. Metrics were transformed in various ways (see Methods); best ANOVA fitting transformation listed for each metric.

Complementarity effect, n=165, no transformation

Source	df	SS	MS	F	p
block	2	1649.0	824.5	0.2	0.80
richness (2 or 6)	1	18228.1	18228.2	5.0	**0.02**
env treatment	3	71484.5	23828.2	6.6	**0.0003**
richness:env treatment	3	12977.9	4326.0	1.2	0.31
residual	155	561352.3	3621.6		

Sampling effect, n=161, relativized and square-root transformed

Source	df	SS	MS	F	p
block	2	3.8	1.9	5.8	0.004
richness (2 or 6)	1	0.0	0.0	0.1	0.79
env treatment	3	3.5	1.2	3.5	**0.016**
richness:env treatment	3	0.3	0.1	0.3	0.85
residual	151	49.7	0.3		

Net biodiversity effect, n=168, no transformation

Source	df	SS	MS	F	p
block	2	24665.6	12332.8	3.8	0.02
richness (2 or 6)	1	37145.9	37145.9	11.5	**0.0008**
env treatment	3	48662.0	16220.7	5.0	**0.002**
richness:env treatment	3	6341.7	2113.9	0.7	0.58
residual	158	508873.0	3220.7		

Table 4.6. Mean relative yields for each species (except SAHO) in HS (high fertility, shaded) and HU (high fertility, full sun) environments, arranged in order of tallest to shortest height in mixture. Positive HU-HS values indicate enhanced relative yield with full sun treatment; note that all subcanopy species have positive values while the tallest species, *F. esculentum*, has a drastically reduced relative yield when shaded.

Species	HS	HU	HU-HS
FAES	0.69	0.29	- 0.40
LIUS	0.40	0.64	+0.24
AMHY	0.50	0.65	+0.15
BOOF	0.11	0.19	+0.08
CAOF	0.39	0.59	+0.20
ACMI	0.16	0.39	+0.23

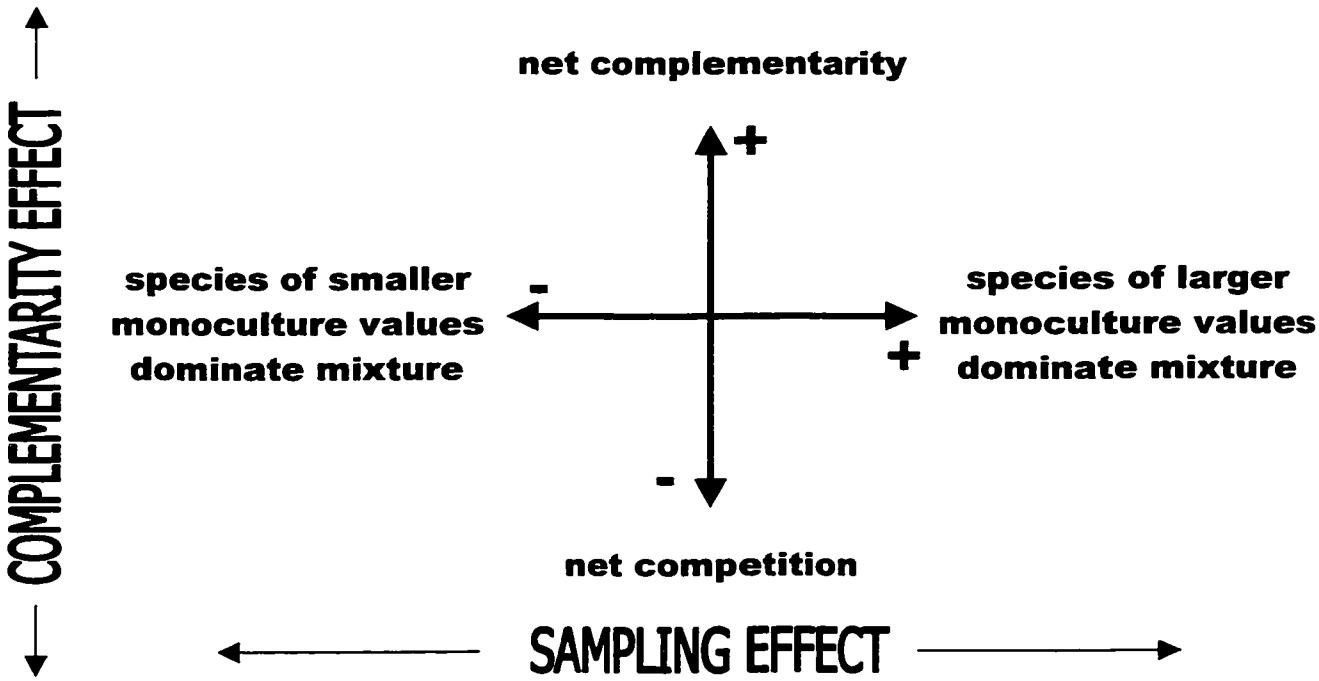

Figure 4.1. Ecological meanings of the complementarity and sampling effects, as suggested by Loreau and Hector (2001).

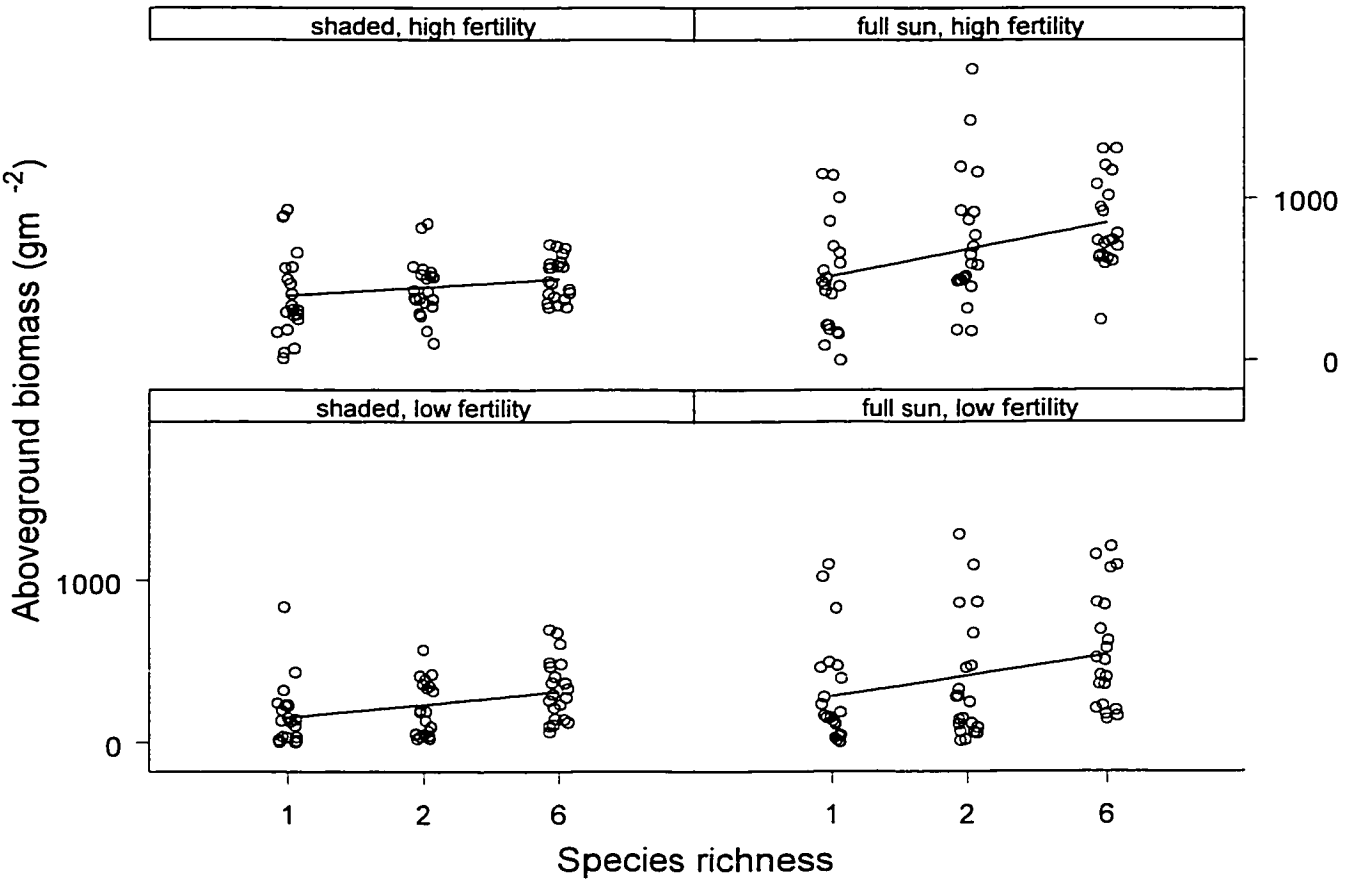

Figure 4.2. The effect of species richness on aboveground biomass in each of the four unique environments created by low and high soil nutrient levels (fertility) and full sun and shaded light treatments. Values are jittered along the x-axis for clarity.

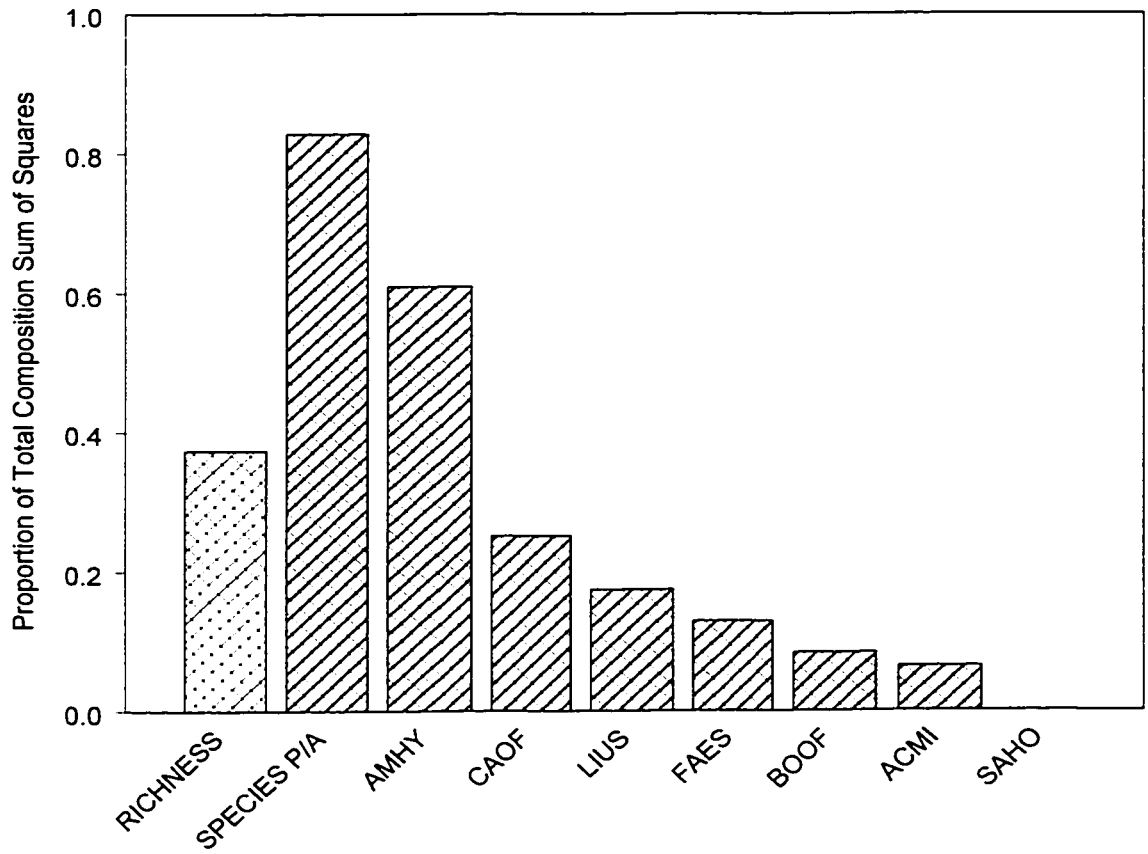

Figure 4.3. Variation in aboveground biomass explained by different components of species composition, listed as proportion of total composition sum of squares explained by a component. "Species P/A" is the SS accounted for by species identity alone, i.e., without species interactions. Species terms describe the variation accounted for by the presence or absence of that species, coded as a dummy variable in ANOVA. All terms were fitted to the ANOVA model by themselves, immediately after the composition factor.

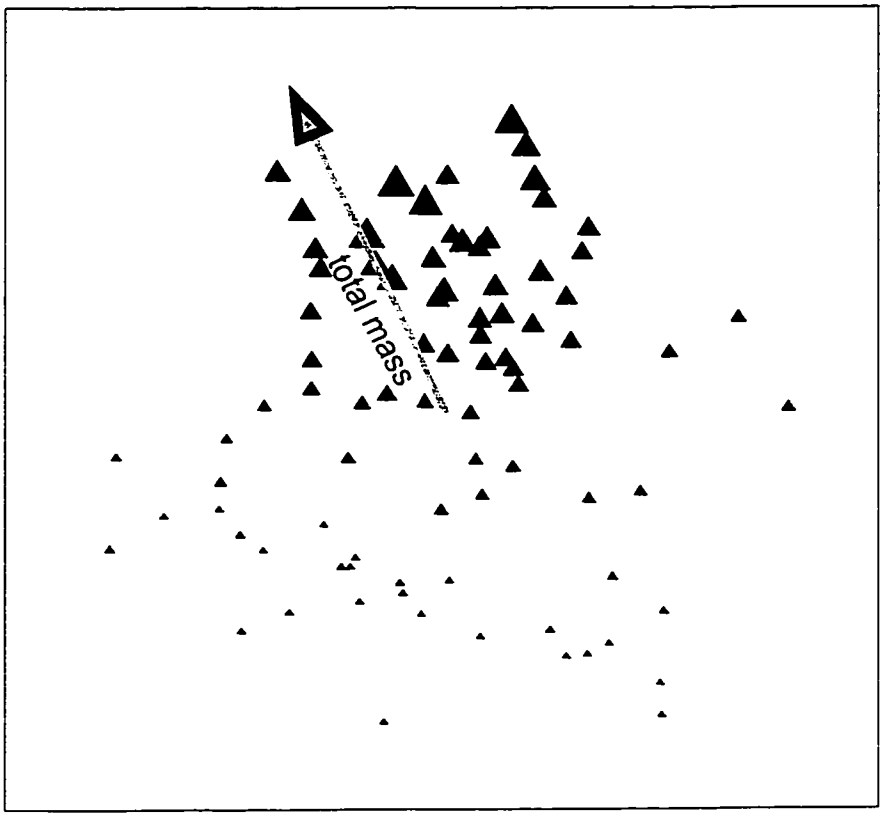

Figure 4.4. Non-metric multidimensional scaling ordination of final species composition for all plots, weighted by abundance of *A. hypochondriacus*. The gray arrow indicates a total mass vector, suggesting a close correlation between *A. hypochondriacus* abundance and total plot mass. Final composition was not clearly related to environmental treatment. Details of the ordination are given in the text.

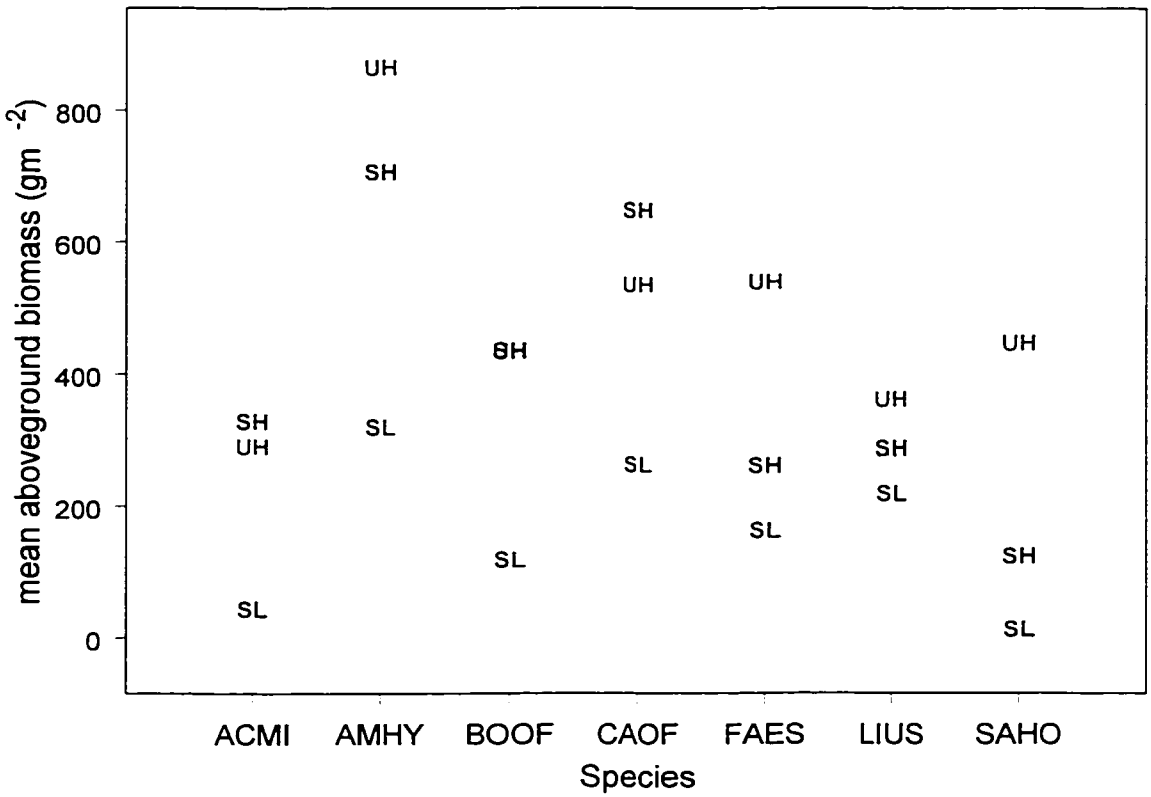

Figure 4.5. Mean monoculture biomass of each species in each of the four environmental treatments; SL = low fertility, shaded; UL = low fertility, full sun; SH = high fertility, shaded; UH = high fertility, full sun. Species abbreviations are listed in Table 1.

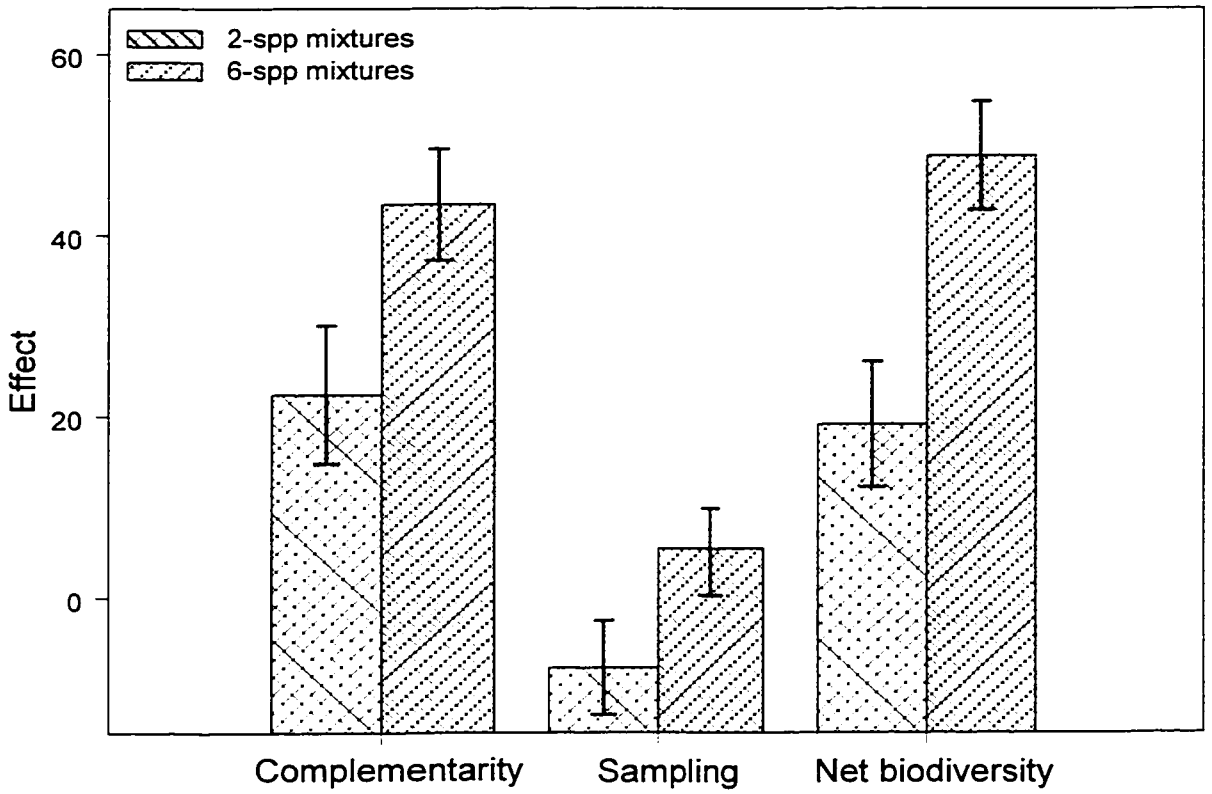

Figure 4.6. The effect of initial richness of mixtures (2 or 6) on complementarity, sampling, and net biodiversity effects. Error bars indicate one standard error of the mean.

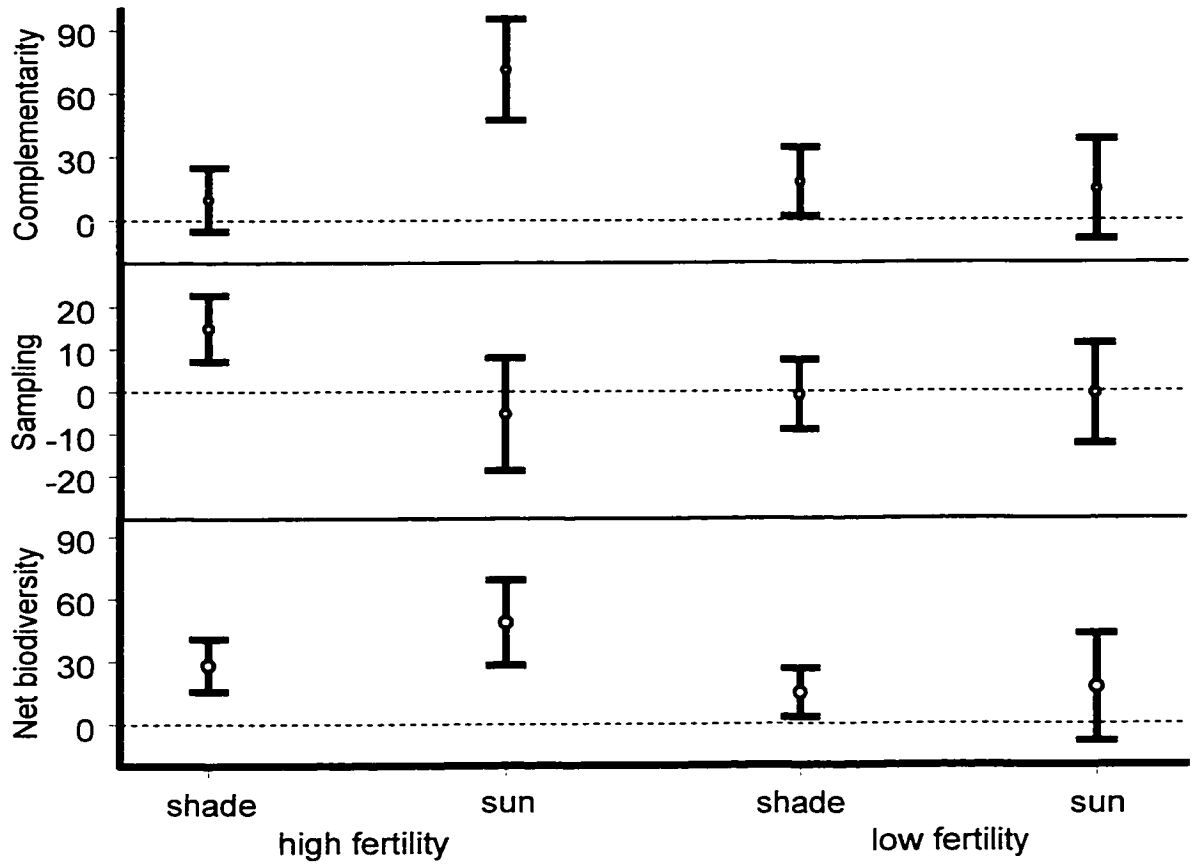

Figure 4.7. Complementarity, sampling, and net biodiversity effects summarized by environmental treatment. Median values are indicated by circles and error bars are 95% confidence intervals of the median. Y-axis scaling differs by effect; zero is indicated by the dashed lines.

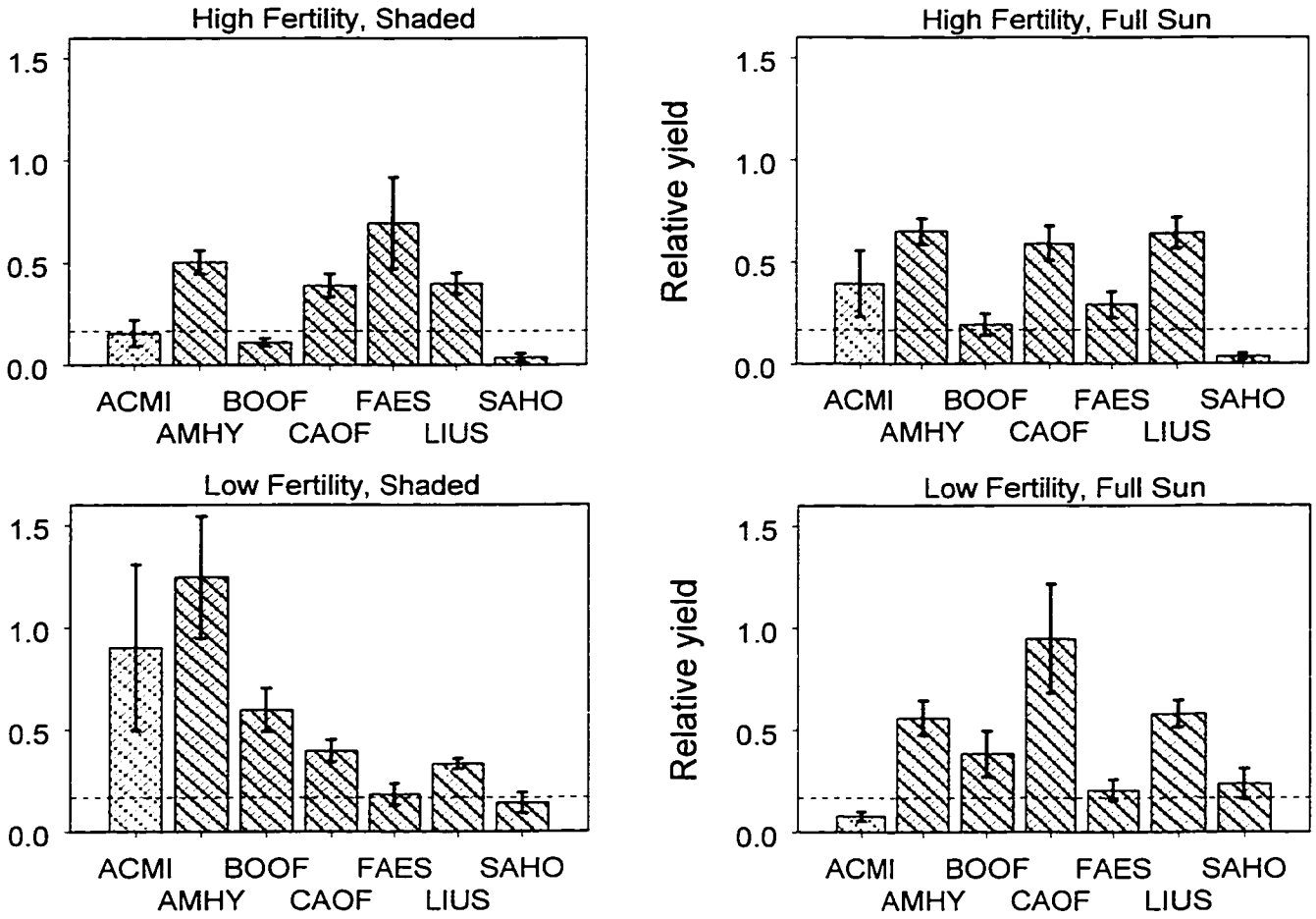

Figure 4.8. Relative yields (specific mixture mass / monoculture mass) for each species in each of the four environmental treatments (+/- s.e.). Values greater than 1/6 (dashed lines) indicate a species performed better than expectation. Species abbreviations are listed in Table 1. Note the high relative yields of ACMI and AMHY in the low fertility, shaded treatment and that of CAOF in the low fertility, full sun treatment.

Chapter 5

Plant interaction models, biodiversity effects, and the niche concept

Abstract

Several researchers have provided theoretical extensions of concepts derived from experimental studies of the relationship between species diversity and ecosystem productivity. However, few if any prevailing models of this relationship provide predictions of how diversity effects might change with environmental conditions such as resource availability, and none have explicitly considered the relationship between diversity effects and mechanisms of species coexistence. Here I use three different modeling techniques of species interactions to extend the theoretical basis for understanding diversity effects and especially to incorporate results of prior experimental studies. The first model is a non-mechanistic descriptor of plant competition that provides precise definitions of competition, complementarity, and facilitation; these definitions are then used to explore how the nature of pairwise species interactions influences diversity effects on plant mixture yield. The second model is the MacArthur-Tilman resource ratio model, which I use to generate predictions of how resource supply rates influence diversity effects by controlling resource partitioning and dominance relations in two-species competition at equilibrium. I then use the classic Lotka-Volterra competition equations to derive these same predictions for dynamic systems away from equilibrium where diversity is maintained by intermediate disturbance levels. Together,

these three modeling techniques reveal that diversity effects should be strongly affected by resource availability and whether species coexist by resource partitioning or non-equilibrium dynamics. The models also demonstrate that the "complementarity" versus "sampling effect" distinction in diversity-productivity studies is perhaps the latest manifestation of the "dual niche" concept, where species are defined by their resource requirements versus their impact on their environment. This dual niche concept has appeared in many manifestations in community ecology, and provides an important link between diversity-productivity studies and the colorful conceptual history of research of species interactions.

Introduction

Theoretical models of the relationship between species diversity and ecosystem functioning were quick to follow the earliest experimental evidence suggesting plant diversity enhances ecosystem productivity (Tilman et al. 1997a, Loreau 1998, Naeem 1998, Loreau 2000, Petchey 2000). However, those models concerned specifically with the influence of plant diversity on ecosystem productivity provided little more than a demonstration of the nature of complementarity versus sampling effects (e.g., Tilman et al. 1997a, Loreau 1998), and many important yet unexplored aspects of the diversity-productivity relationship remain. For example, complementarity and sampling effects have generally been explored in separate models (e.g., Tilman et al. 1997a, Petchey 2000), and it is unclear whether they interact to control the functioning of plant communities. This may be especially important along a resource availability axis where certain species are expected to dominate mixtures and cause local species extinction, but

resource competition dynamics have yet to be included in diversity-productivity models. Moreover, despite the parallelism between the influence of diversity on productivity and mechanisms that allow for species coexistence such as resource partitioning, there has been no attempt to connect classical models of species coexistence with models that describe how greater levels of coexistence may influence ecosystem functioning.

A modeling treatment of diversity effects on productivity that is explicitly tied to resource competition would also provide contextual support for several previous experimental studies of the diversity-productivity relationship. I performed two such studies along resource gradients that strongly suggest that diversity effects are sensitive to environmental context. It is unclear, however, how these results are to be extrapolated to the wide range of community types and environmental conditions found in both natural habitats and agroecosystems. A major limitation is the limited duration of these types of experiments (both about 3 months) and the pragmatic requirement for a mostly annual species pool. Annual species should not be expected to exhibit the same range of resource partitioning as a group of perennials, for example, nor should the classic dominance relationships often found in sites of high productivity be expected to establish among annuals, which are instead adapted for rapid colonization of more disturbed sites where dominance relations are precluded (Grime 2001). Thus, the results of these short-term experiments might be underestimating both potential complementarity effects and sampling effects, and hence not be an accurate representation of how biodiversity effects should change along resource gradients in more perennial systems.

I present in this chapter three different modeling techniques that provide theoretical extensions of prior experimental results and new predictions of relationships

between diversity effects, resource availability, and mechanisms of species coexistence. Each technique uses an established model of species interaction that was initially used for another purpose: one to model plant competition experiments and the other two to model mechanisms of species coexistence. Each model is easily adapted to simulate biodiversity experiments—all that is required are monoculture values for each species (i.e., their carrying capacity, or density when grown without competitors at particular resource position) and the yields (density) of each species in competition. These simulations are then mechanistically analyzed using the same techniques employed in real experiments—for simplicity I use the Loreau and Hector (2001) additive partition technique to attain estimates of complementarity, sampling, and net biodiversity effects for each "experiment". Note that the treatment of sampling effects with this technique most closely approximates the "performance sampling effect" (Chapter 2), and other aspects of sampling effects, such as the higher probability of including particular combinations of species at higher diversity levels, are not explicitly considered.

Within the context of their assumptions, the models reveal how ecosystem productivity may be affected by species diversity, whether through *performance sampling effects* (hereafter "sampling effects"), where dominance relations inflate (or deflate!) average mixture yields, *complementarity*, where species are required to partition resources and thus use them more fully in mixture, and even *facilitation*, where species attain greater individual yields next to interspecific neighbors. The models also reveal that the effects of species on their environment are described by only two sets of parameters—one describing resource requirements, the other describing impacts of species on their environment. The distinction between these two dimensions of a species

niche is in fact just one of the more recent perspectives of a long history of the "dual niche" concept in community ecology, and may provide a more realistic basis for simulating the effects of species extinctions on ecosystem functioning.

Non-mechanistic plant interaction: biodiversity effects and competitive coefficients

A simple non-mechanistic model of plant competition will serve to introduce how biodiversity experiments can be related to established theories of species interaction, especially the nature of plant competition. This first model is the classic hyperbolic competition model, successfully used to describe competitive plant interactions in many studies (e.g., Watkinson 1984; Firbank and Watkinson 1985, 1986; Law and Watkinson 1987; Pacala and Silander 1990; Rees et al. 1996; Freckleton and Watkinson 1997, 2000, 2001). The model is a yield-density form of a Lotka-Volterra-type species interaction model (Hastings 1997) predicting the mean performance of an individual of species i interacting with n neighbor species:

$$\overline{w}_i = \overline{w}_{\mathrm{m},i}[1 + a_i(N_i + \sum_{j=1}^{n} \alpha_{ji} N_j)]^{-1} \qquad (1)$$

where $\overline{w}_{\mathrm{m},i}$ is the mean maximal performance of an individual of species i (without neighbors) at a particular environmental position (analogous to carrying capacity), a_i describes the effects of intraspecific competition, N_i is the mixture density of species i, and α_{ji} is the competitive equivalence coefficient, measuring how many individuals of species i to which each individual of species j is equivalent. Equivalence coefficients have been found to be invariant over a range of densities (Freckleton and Watkinson 1997). The parameter a_i is strongly correlated with $\overline{w}_{\mathrm{m},i}$; the reciprocal of a_i can be

thought of as the density at which the effects of intraspecific competition become important.

The interaction matrix and mechanisms of biodiversity effects

The competitive equivalence coefficients, or alphas, when put into a "community matrix" (Levins 1968, Vandermeer 1970, Freckleton and Watkinson 2001) in which the value of row i column j describes the per-capita effects of species j on species i, describe the intensity and direction of all pairwise interactions among the n species in mixture. From the perspective of biodiversity experiments, the community matrix is interesting because it provides a summary of all pairwise interactions, be they competitive, complementary, or even facilitative. Indeed, the community matrix reveals how complementarity and facilitation can be separated in biodiversity experiments, a considerable obstacle in mechanistic treatments of biodiversity effects (Fridley 2001, Loreau and Hector 2001). Recall that all interspecific interactions are scaled to the effects of added individuals of a target individual's own species (i.e., alphas in the diagonal of the interaction matrix equal 1). Therefore, all alphas that are greater than 1 indicate competition, where the addition of a different species reduces the yield of a target species more than that of its own species. Alphas less than 1 indicate greater yield of a target species when surrounded by a different species compared to that of its own species. This is indeed the definition of complementarity (Trenbath 1976, Vandermeer 1989, Hooper 1998, Fridley 2001), which may cause overyielding (de Wit 1960, Trenbath 1978, Vandermeer 1989, Jolliffe 1998) perhaps as a result of resource partitioning where species use different environmental resources. When alphas equal

zero, the addition of a new species has no effect whatsoever on the target species, which indicates perfect complementarity (i.e., no niche overlap; Colwell and Futuyma 1971, May and MacArthur 1972). Finally, negative alphas indicate that the yield of a target species is *enhanced* by the addition of a different species. In the model, this operates by reducing the sum of the denominator (to a limit, however, of $[a(N_i+\alpha N_j)-1]$, above which yield is undefined). Performance enhancement above what an individual can attain without any neighbors (zero density) is a convenient and precise definition of facilitation (but one of many that exist; see Vandermeer 1989, Callaway 1995). Positive biodiversity effects on productivity may be caused by any alpha value less than 1 (see below): complementarity then becomes the case where alpha is between 0 and 1, and facilitation is the case of negative alpha. The relationship between alpha and biodiversity mechanisms can be summarized as:

$$\text{Facilitation} < (\alpha = 0) \leq \text{Complementarity} < (\alpha = 1) \leq \text{Competition}$$

A particularly important point for biodiversity experiments is that the separation of complementarity and facilitation will be difficult if not impossible unless species are grown without neighbors so that $\overline{w}_{m,j}$ can be estimated.

The influence of particular values of alpha in the interaction matrix on biodiversity effects in mixture experiments can be easily simulated with the model, and the results of a replacement series experiment with N interacting species can be mechanistically analyzed with the "additive partition" technique of Loreau and Hector (2001) (discussed in detail in Chapter 4). For the purposes of the present discussion,

recall that the technique gives estimates of the "net biodiversity effect," defined as the deviation in mixture yield from its expected yield based on monoculture values. The net biodiversity effect (BE) is then partitioned into two quasi-independent components: the complementarity effect (CE), which estimates overyielding (resulting from complementarity, facilitation, or both); and the sampling effect (SE), which measures the covariance between species' mixture dominance and monoculture values (and thus does not include the sampling of particular species combinations). To determine how different values of alpha influence biodiversity effects in mixture experiments, I simulated three biodiversity experiments using 10, 5, and 2 species, all of equal monoculture performance (carrying capacity) and varied the mean interaction coefficients (alphas). For each simulation of different mean alpha, I calculated BE of the mixtures using the additive partition technique. Note that in the case where all monoculture values are equal, SE = 0 and BE = CE.

Figure 5.1 shows the exponential decay of BE as the mean value of the community matrix increases. There are four important points evident in this graph. First, small differences in mean alpha have far greater effects on BE in the region of facilitation than that for complementarity, suggesting that truly facilitative interactions (alphas<0) should lead to much greater biodiversity effects on productivity than complementary interactions. This may explain why the most pronounced effects of so many diversity-productivity experiments are the result of including legumes in species-rich mixtures, where neighbor species may perform better next to N-fixers than they do when grown in isolation (Tilman et al. 1997b, Hooper 1998, Hector et al. 1999, Loreau and Hector 2001, Fridley 2001). Second, even within the alpha region of complementarity, the relationship

between the degree of complementarity between species and the resulting effects of diversity on production is not linear, such that a small degree of complementarity (e.g., alphas between 1 and 0.5) may not cause detectable relationships between diversity and productivity. Third, the effects of increasing levels of species richness are most prominent at high levels of complementarity, and especially when the mean alpha value indicates facilitation. This further demonstrates that effects of diversity on yield should only be manifest at relatively high levels of complementarity (and facilitation). Finally, biodiversity effects become negative when the mean alpha lies in the region of competition (alpha>1). Determining the reason for this requires a more detailed look at the alphas in the context of "reciprocal" relationships between species.

Biodiversity effects and interaction reciprocity

Interactions between species in the community matrix are described both by the effects of species *j* on species *i* and vice-versa, and there is no simple expected relationship between α_{ji} and α_{ij}. There have been recent attempts to determine whether α_{ji} and α_{ij} should be inversely related for competing plants, which have been called "reciprocal" competitive relationships (Freckleton and Watkinson 2001). The reasoning is that if species A has a high competitive effect on species B ($\alpha_{AB}>1$), perhaps due to a higher apical growth rate by which it usurps available light, then species B should have comparatively little effect on Species A ($\alpha_{BA}<1$). A perfectly reciprocal competitive relationship is defined as:

$$\alpha_{ji} = 1/\alpha_{ij} \qquad \text{(reciprocal competition)} \qquad (2)$$

where one of the alphas is greater than 1. In other words, reciprocal relationships require competitive effects to be coupled to complementary effects by asymmetric competition. Importantly, reciprocal competitive relationships translate to alphas in a community matrix having a mean value of 1. As shown above, species mixtures of equal monoculture values (i.e., no sampling effect possible) cannot exhibit biodiversity effects (positive or negative) if the mean of alphas is 1. Figure 5.2 shows the effect of reciprocal pairwise alphas on the net biodiversity effect for a mixture of 2 species. There is no significant BE with reciprocal alphas. Like that of Figure 5.1, α_{ji} varies from greater than 1 to negative values, but here α_{ij} equals the reciprocal of α_{ji} (with a small amount of normal error; i.e., $\mu = 1/\alpha_{ji}$; s.d. = $0.1/|\alpha_{ji}|$). (Small error is required, because it actually turns out that reciprocity is only an approximation of the "cancellation effect" of competitive and complementary relationships; *perfect* reciprocity between pairwise alphas yields slightly negative BE values, but small deviations in the reciprocal relationship above and below the alpha relationship of equation (2) yield slightly negative and slightly positive BE values, respectively. The actual solution to the relationship between pairwise alphas that yields perfect cancellation (zero BE) is a complex function listed in Appendix A.)

If all pairwise species interactions are reciprocal (competition equaled by complementarity), there will be no effect of diversity on productivity. This "cancellation" effect has been documented in intercropping experiments using the Relative Yield Total (RYT), where the greater-than-expected relative yields (mixture yield/monoculture yield) of certain species is "canceled" by lower-than-expected values for other species in mixture, leading to RYT = 1, or no mixture yield advantage. When

the mean of alphas is greater than 1, complementary and competitive relationships are not canceled out and the net result is competition. Here, because species on average perform poorer next to different species relative to their own species, net competition is in fact "interference" competition, where species A negatively affects species B *and* species B negatively affects species A. This is the classic case of "underyielding" (Trenbath 1974, Vandermeer 1989), which may be due to allelopathy, though it is uncommon in cropping experiments and perhaps even in natural plant communities (Harper 1977, Trenbath 1978). In this new context of the community matrix, underyielding is seen as a non-reciprocal competitive relationship (if between two species) or a mean alpha value greater than 1 (for a suite of interacting species). Underyielding causes complementarity effects to be negative in the Loreau and Hector additive partition (see Chapter 4); hence, this is why net biodiversity effects become negative at mean alphas greater than 1 in Figure 5.1.

The concept of interaction reciprocity can be extended to complementary and facilitative relationships as well. Indeed, the interaction between two species cannot be defined on the basis of one of the pairwise alphas alone; for interactions to be labeled "competitive," "complementarity," or "facilitative," the relationship *between* the pairwise alphas must be considered. This suggests that if either of the two alphas that describe a pairwise interaction is greater than 1, the relationship should be described as competitive—if both alphas are greater than 1 this indicates interference competition, while reciprocal alphas suggest the more common exploitation competition. Second, "complementary" species should be defined as the case where *both* alphas are between 0 and 1, and "reciprocal complementarity" a subset of these interactions where alphas are equal:

$\alpha_{ij} = \alpha_{ji}$ (reciprocal complementarity, alphas between 0 and1)

The same relationships can be defined for facilitation, although dual-facilitative relationships (where both alphas are less than 0) are probably extremely rare in plant communities (Callaway 1995) and probably better apply to multi-trophic interactions. Table 1 lists the summary of definitions for species interactions based on interaction coefficients.

Biodiversity effects and higher-order interactions

The community matrix of the hyperbolic competition model describes the intensity of all possible pairwise interactions; as such, it does not account for multi-way interactions among several species. Such interactions, where, for example, the presence of species C changes the interaction between species A and B, have been termed "indirect" (Miller 1994) or "higher-order" interactions (Hairston et al. 1968, Billick and Case 1994); by definition, they cannot be predicted from a pairwise community matrix. One might well ask if studies investigating the influence of biodiversity on ecosystem processes are in effect trying to determine whether biodiversity effects are primarily the result of "zero-order" effects (the presence or absence of particular species alone), "first-order" effects (predictable based on pairwise species interactions, such as complementarity), or higher-order effects. Note that even if higher-order interactions are irrelevant, the most species-rich mixture could outyield any subset mixture (if every species inhabits a unique niche, for example). Higher-order interactions, however, can promote diversity effects even if pairwise interactions are all competitive. For example, "direct" facilitation is where the presence of one species enhances the performance of a

neighbor species, and can be described by a first-order interaction model. However, "indirect" facilitation has been described as the case where two species compete (say, A and B), but the presence of a third species (C) reduces these competitive effects, such that the measured effects of species C on A and B are positive even though they might be negative when species A or B is absent (Miller 1994; see also treatments of "indirect mutualism," Vandermeer and Boucher 1978, Vandermeer 1980).

The detection of higher-order interactions is notoriously difficult (Case and Bender 1981), and incorporating such complex interaction networks into biodiversity experiments will require enormous resources. Consider just the investigation of potential 3-way interactions (i.e., how the presence of each species changes the pairwise interaction of each possible pair). In an experiment with 10 species, the 10 x 10 interaction matrix could be expanded into a 10 x 10 x (10-2) array, where the third dimension describes how each of the 90 pairwise interactions is changed by the presence of each of the eight remaining species. Experimentally, this would require growing each possible mixture of 2 species (45 plots) and each possible three-species combination (120 plots), which, even without replication is a large undertaking. Every possible species combination, including monocultures, for *n* species is

$$\sum_{i=1}^{n} \frac{n!}{(n-i)!\,i!}$$

For an experiment using 10 species, this equals 1023 plots, without replicates! Multi-dimensional arrays could be used as "community arrays" to describe all first- and higher-order interactions. But clearly the detection of higher-order interactions in biodiversity experiments is, for now, strictly within the realm of modeling.

Competition for resources: resource ratios and consumption vectors

The non-resource-based competition model showed how diversity-productivity relationships might be predicted from separate estimates of the interactions between species pairs, assuming no higher-order interactions are involved. But because no explicit treatment of competition for resources was included in this model, there is no straightforward way to use it to predict how diversity-productivity relationships may change under different environmental contexts, which was the principal motivation behind prior experimental studies (Chapters 3 and 4). To couple diversity effects to environmental context, species interactions must somehow be connected explicitly to environmental parameters. One way to do this is to have species compete for resources that are, in turn, affected by changes in species population sizes. This calls for the use of two differential equations—one describing the dependence of the per capita growth rate of a species on resource levels, the other describing changes in resource levels with changes in species population size. This is in effect the classic Lotka-Volterra predator-prey model made explicit for resource competition by MacArthur (1972) and further developed specifically for resource-based plant competition by Tilman (1982, 1988). In this section, I use the basic MacArthur-Tilman model to explore how diversity-productivity relationships change with resource supply conditions. Here I explore biodiversity effects at equilibrium; in the next section I explore these effects away from equilibrium.

The basic resource ratio model

A simple form of the resource ratio model demonstrates, in terms of explicit resource competition, the conditions necessary for the equilibrium coexistence of two species competing for two essential (i.e., non-substitutable) resources (Tilman 1982). Each species displays Monod-type population growth above the concentration of resource where growth rate equals mortality rate; this resource level, below which a species cannot maintain positive growth, is called R*. Displayed on a phase-plane of the levels of two independent resources, the region in which a species exhibits positive or negative population growth is described by a "ZNGI", or zero-net growth isocline (Figure 5.3). One criterion for coexistence is that species' ZNGIs overlap; that is, one species is more limited by resource 1, for example, and the other is more limited by resource 2. This is in fact equivalent to complementary resource use between species, because species A can take advantage of a particular resource supply region that species B cannot, and vice-versa. But this is not the only criterion for stable coexistence.

The other aspect of the model that determines the equilibrium outcome and whether species coexistence is stable is the rate at which resources are supplied and the rate at which each species consumes each resource, called "consumption vectors". The consumption vector for a species is the vector sum of the rate at which it consumes each resource (Figure 5.3). For coexistence at equilibrium to be stable, each species must consume relatively more of the resource that limits its own growth rate—that is, if species A has a higher R* for resource 1 than resource 2, it will stably coexist with species B if its consumes more of resource 1, species B has a higher R* for resource 2 *and* species B consumes relatively more of resource 2 (assuming an appropriate resource

supply point in the first place; see below). This is equivalent to the criterion for equilibrium coexistence in the Lotka-Volterra competition model: each species must limit itself more than it is limited by the other species (competitive alphas must be less than 1). Note also that consumption rates and carrying capacities are inversely related in this model; in other words, all else equal, species with higher consumption rates for a particular resource have lower monoculture densities (yields) because they require more resource to attain a given density.

In terms of diversity-productivity relationships, all this translates into two important points: 1) the existence of complementarity is determined by overlapping ZNGIs, but only if coexistence occurs (i.e., consumption vectors lead to stability), and 2) consumption vectors determine a species' monoculture yield (but inversely). Therefore, by varying ZNGI distributions (or levels of complementarity, similar to varying alphas above) and consumption vectors (or the level of potential sampling effects), the resource ratio model can be used to investigate diversity-productivity relationships. Most importantly, these relationships can be explored over a range of resource supply points to predict whether resource levels should change the effect of diversity on yield.

For the analysis described below, I used the analytical solution of population sizes (=mixture yields) at equilibrium for two-species competition from Tilman (1982) (listed in Appendix B along with parameter values). The resulting mixture and monoculture yields derived from the model were then analyzed with the Loreau and Hector (2001) additive partition method, described above, to determine the effect of different rates of resource supply on complementarity effects (CE), sampling effects (SE), and net biodiversity effects (BE). As discussed in detail in Chapter 4, the additive partition

metrics are highly sensitive to total mixture yield and so are difficult to compare among sites of different resource levels. Below, I report both absolute partition values and "relative" values where each of the three metrics is divided by the total mixture yield. Note that these results for two-species competition can be extended to mixtures of more species only if resource heterogeneity is included in the model, as only two species can coexist on two resources at equilibrium at one resource supply point (see Tilman and Lehman 2002).

Biodiversity effects along resource gradients under stable coexistence

Figure 5.4 shows the sensitivity of CE, SE, and BE to resource supply rate for a mixture of two species that exhibit complementary resource use (overlapping ZNGIs) and have consumption vectors where each species consumes more of the resource that limits itself. This configuration leads to stable coexistence for the resource supply points located within the consumption vectors (dashed lines). Complementarity effects only occur within the resource supply region that defines coexistence—i.e., for complementarity to occur, both species must be present at equilibrium. Furthermore, CE increases up the "spine" of dual resource enrichment because CE is sensitive to the average monoculture value, which increases when both resources are added. This effect is removed when CE is measured relative to average monoculture value. Moving from the center of the coexistence region outward toward either axis, CE declines because species are less able to partition resources.

Sampling effects, on the other hand, dominate the region outside coexistence, where one species completely dominates the mixture. Interestingly, sampling effects also

occur within the coexistence region, because slight dominance relationships are created when the supply of the two resources is not equal (in terms of coexistence, this means the equilibrium resource point does not lie on the ZNGI intersection). Along each resource gradient, sampling effects are unimodal, peaking shortly before coexistence regions before becoming zero where resource supplies of each resource are equal. This results from a trade-off where sampling effects are enhanced by the monoculture yields of each species (which is increased by resource supply), but decreased by stable niche partitioning, the region of which becomes larger as resource supply increases. Furthermore, SE is always positive in this scenario because the species that ends up "winning" or dominating a mixture is the species with a greater monoculture value for a given resource supply point.

Biodiversity effects along resource gradients under species dominance

If biodiversity effects are to occur outside the necessary conditions for species coexistence, the intuitive expectation is that complementarity disappears and is replaced by sampling effects. Indeed, complementarity is coupled to coexistence, but the sampling effect may occur under various degrees of coexistence or complete dominance. A more interesting question is whether sampling effects from dominance are predicted to be sensitive to rates of resource supply, and which conditions lead to positive versus negative sampling effects. An easy way to examine dominance-based sampling effects along resource gradients with the resource ratio model is to have one species dominate over all resource supply points at equilibrium—i.e., R*s for one species are below both R*s for its competitor (ZNGIs non-overlapping) and one species has a higher

consumption rate for both resources. Figure 5.5 illustrates these scenarios. In the first case (graph A), the wining species (with the lower R*s) also has the higher carrying capacity for all resource supply points (or monoculture yield, inversely related to its consumption rate). Here performance sampling effects are positive and increase with added supply of both resources (to increase mixture yield, resources must be added together or one will still limit growth). This is true even when SE is measured relative to mixture yield (not shown). SE is positive everywhere because the larger species always dominates, so mixture yields are always greater than the expected average of the two species. SE increases with resource supply because the difference between the average monoculture vales and the total mixture yield (of the dominant species) increases with added resource. In the second dominance scenario (Figure 5.5B), the winning species has a lower carrying capacity (or higher consumption rate for both resources), which leads to a negative sampling effect at each resource supply point. By the same means as scenario A, mixtures yield below the average of the monoculture yields because the least productive species dominates (see also Figure 4.1), and SE continues to decrease with dual resource enrichment.

It is also possible that the relative carrying capacities of two species depend upon resource supply points, such that in one resource supply region species A has a higher monoculture value, and in another region species B has a higher monoculture value. Here, even if one species eventually came to dominate at equilibrium over all resource supply points (because it had lower R*s for both resources), whether total yield is increased or decreased by richness depends upon resource levels. This case is illustrated in Figure 5.5C, where species A consumes relatively more of resource 1 and species B

consumes relatively more of resource 2, but species A dominates for every resource supply point. In the lower resource supply region where species A has a higher monoculture value, sampling effects are positive, but these become negative in the upper region where species B has a higher monoculture value. As before, complementarity is impossible because ZNGIs do not overlap, so net biodiversity effects equal sampling effects.

Summary of resource ratio model predictions

The equilibrium outcome of two-species competition under a range of different resource supply points and different conditions of coexistence and dominance allows several predictions of how diversity-productivity relationships may change along resource gradients. Note that the following predictions are based on the rather restrictive assumptions of the model, including equilibrium population densities and resource levels, no resource heterogeneity, no major differences in life-history or phenology among species, no trophic interactions, etc.

First, complementarity is a mechanism of equilibrium coexistence; simple resource partitioning is not enough to generate complementary relationships if species cannot coexist at equilibrium at a certain resource supply point. At the very least, this suggests that a complementary relationship at one resource level may cease to exist under another set of resource conditions. Complementarity should increase within the set of conditions required for coexistence as conditions become most optimal for resource partitioning—i.e., as population densities (yields) become most equable. In other words, complementarity may be as dependent upon species evenness as species diversity

(Wilsey and Potvin 1999). Within this coexistence region, complementarity effects should be greater than sampling effects, particularly as evenness increases (and dominance relationships disappear).

Second, sampling effects should always be present unless conditions for coexistence are met *and* species do not dominate mixtures any more than the proportion of their initial planting density. In one sense this is circular reasoning because SE is calculated as the covariance between monoculture yield and deviation of relative yield (or dominance if positive) by the Loreau and Hector metric. It makes intuitive sense, however, that sampling effects only occur when dominance relationships are created in mixture (see also Chapter 4). Outside the conditions for coexistence, sampling effects are inevitable because, by definition, dominance emerges. Positive sampling effects (leading to positive biodiversity effects) will occur when, for a particular resource position, the winning (or simply dominant) species has a higher-than-average monoculture yield (or carrying capacity), while negative SE occurs when the winning species has a lower-than-average monoculture yield. As with CE, such relationships may depend on resource levels, particularly when relative carrying capacities are sensitive to environmental parameters.

How should these predictions change when the assumptions of the model are violated? Resource heterogeneity enhances the probability of species coexistence and allows for more species to coexist at equilibrium on as few as two resources (Tilman 1982, Pacala and Tilman 1994). It is therefore reasonable to expect complementarity to increase with resource heterogeneity given that species are able to partition this enlarged resource space. As resource partitioning increases, species dominance should decrease,

which should lower the degree to which sampling effects determine diversity-productivity relationships. (For an application of the resource ratio model to the diversity-productivity relationship with mixtures of more than two species where resource heterogeneity is utilized, see Tilman and Lehman (2002), although they do not simultaneously explore complementarity and sampling effects in the same model, and do not mechanistically explore their simulations with the additive partition technique.) Life-history differences should strongly enhance the potential for resource partitioning and hence complementarity, and indeed phenological differences among experimental species have provided some of the largest effects of diversity on production in prior studies (e.g., Hooper and Vitousek 1997, Tilman et al. 1997b, Hooper 1998). Perhaps most importantly, the assumption most clearly violated in plant diversity experiments is that populations and resources have attained equilibrium levels in short-term experiments (particularly in assemblages of annual crops!). It is therefore useful to briefly explore how relaxing the equilibrium assumption changes the predictions of the resource ratio model.

Biodiversity effects away from equilibrium

Discussion over the degree to which species coexistence is a result of equilibrium versus non-equilibrium processes has a long and colorful history in ecology (reviews by, for example, Armstrong and McGehee 1980, Schoener 1982, Chesson and Case 1986, Huston 1994, Grace 1999, Hubbell 2001). For species to coexist at equilibrium (ignoring trophic interactions), they must partition resources in a way that avoids competitive exclusion, the so-called competitive exclusion principle (Gauss 1934, Vandermeer 1972).

The above resource ratio model is a good representation of this perspective, and like the hyperbolic competition model, clearly reveals that biodiversity effects by means of complementarity are directly coupled to processes or factors that control species coexistence *at equilibrium*. But what if species coexist largely because competitive relationships are not allowed to proceed to equilibrium exclusion? Indeed, the paradox that species must have similar resource requirements to inhabit the same habitat but have different resource requirements to avoid competitive exclusion has been one of the prime driving forces of plant community ecology over the past half-century (Hutchinson 1959, Wuenscher 1969, Grubb 1977, Chesson 1986, Ricklefs 1987, Zobel 1997), leading many to suggest that species coexist largely due to, for example, intermediate disturbances (Loucks 1970, Grime 1973, Connell 1978, Huston 1979) and low rates of competitive displacement (Hutchinson 1961, Grime 1973, Huston 1979, Caswell 1982). If species coexist in this manner, what does this mean for expected diversity-productivity relationships? In other words, do biodiversity effects depend fundamentally on how species coexist?

Following Huston (1979), I used the standard Lotka-Volterra competition equations to evaluate how biodiversity effects change with different non-equilibrium conditions, again employing the Loreau and Hector (2001) additive partition technique, which provides separate estimates of complementarity and sampling effects. Dynamic solutions of the Lotka-Volterra model, unlike the equilibrium solution, depend upon the relative growth rates of interacting species. The way in which these rates affect final species diversity, and hence biodiversity effects, is then controlled by two independent factors: the frequency of disturbance, in this case a density independent population

reduction of all species at a certain time interval, and the rate of competitive displacement. Huston (1979) showed how these factors determine dynamic equilibria solutions of species diversity. For simplicity, I keep frequency of disturbance constant at an "intermediate" level and vary the rate of competitive displacement. This axis of competitive displacement rate can be interpreted as a resource gradient, and is often experimentally varied as soil fertility (e.g., Austin and Austin 1980, Campbell and Grime 1992). Details of this simulation, including all parameters used, are listed in Appendix B.

I first examined biodiversity effects of six-species mixtures under intermediate disturbance at different rates of competitive displacement, with no resource partitioning among species (all $\alpha = 1$) and carrying capacities inversely related to per-capita growth rates (the classic *r-K* tradeoff; MacArthur and Wilson 1967). In accord with the dynamic Lotka-Volterra analyses of Huston (1979), variation in the rate of competitive displacement with constant intermediate disturbance resulted in a unimodal distribution of species diversity (measured as e^H) along the displacement rate gradient (Figure 5.6 C). To determine the corresponding biodiversity effects, separated into CE and SE along the displacement rate gradient, I determined the yields of each species without competitors (with a starting density of 6 for each species), used these "monoculture" yields to calculate expected yields of the six-species mixture, and then simulated the yields of each species in mixture (with a starting density of 1 for each species).

Graphs A and B of Figure 5.6 illustrate the sensitivity of complementarity and sampling effects to the displacement rate gradient in the dynamic Lotka-Volterra model. Unsurprisingly, because species do not partition resources (all $\alpha = 1$), no significant complementarity effects were detected. Instead, positive biodiversity effects were

exclusively determined by sampling effects, which increased along the displacement rate gradient. As before, the reasoning is straightforward: as dominance increases along the rate gradient after diversity peaks (toward the low end of the gradient), so too do sampling effects, as the mixture becomes dominated by the species with greater carrying capacities (Huston 1979). (With positively correlated K and r, these relationships hold but SE reaches an early asymptote along the displacement gradient; results not shown). Because the rate of competitive displacement is negatively associated with species diversity over most of the gradient and positively associated with sampling effects, SE, and hence the net biodiversity effect, is negatively associated with species diversity (Figure 5.6 D). This is an important point—an equilibrium model predicts positive association between realized diversity and biodiversity effects because greater amounts of resource partitioning leads to higher complementarity; a non-equilibrium model in which species coexist only by means of intermediate disturbance predicts biodiversity effects only through sampling effects. This makes clear the distinction between initial or "seeded" diversity and "realized" diversity—*realized diversity and biodiversity effects are correlated only when species partition resources.*

Indeed, when resource partitioning is put back into the Lotka-Volterra model, complementarity effects return whether the model is allowed to reach equilibrium or not. Figure 5.7 illustrates the same scenario as that in Figure 5.6 except interspecific competitive coefficients are half of the intraspecific coefficients (all $\alpha_{ij} = 0.5$; all $\alpha_{ii} = 1$). Sampling effects increase along the displacement gradient because dominance still increases along the gradient (graphs B and C of Figure 5.7), but complementarity effects also increase along the gradient, leveling off as realized diversity reaches low values

(graph A). However, as in the resource ratio model, this is probably due to the increased average monoculture values as rates of displacement (for monocultures, simply growth rate) increase, which spuriously inflates CE values. Nonetheless, complementarity and sampling effects act in concert to determine biodiversity effects when both dominance and resource partitioning occur—this is analogous to the stable coexistence solution of the resource ratio model.

In summary, the only real difference between biodiversity effects in equilibrium versus non-equilibrium scenarios is whether species coexistence is controlled by resource partitioning or disturbance. Resource partitioning, if stable, will always give rise to positive biodiversity effects by means of complementarity use of resources which allows mixtures to harvest more total resources than less species-rich assemblages. Species assemblages that have dynamically stable levels of diversity due to disturbance rather than resource partitioning will also exhibit positive biodiversity effects, but due to sampling effects alone. As dominance increases as a result of resource enrichment, sampling effects will increase in both equilibrium and non-equilibrium solutions of the Lotka-Volterra equations. It is less clear whether complementarity will increase with resource enrichment or will remain constant—this relationship is probably better addressed with the use of specific mechanistic models, such as the light partitioning hypothesis put forth in Chapter 4 and the facilitation hypothesis described in Chapter 2.

Very recently, Pacala and Tilman (2002) produced a similar contrast between equilibrium versus non-equilibrium approaches to biodiversity effects using the Lotka-Volterra equations; they suggested that initial non-equilibrium conditions of biodiversity experiments should be dominated by sampling effects, which over time change into

complementarity as competitive relationships rather than relative growth rates dominate community dynamics. Given that niche complementarity among species exists in the first place, the modeling technique used in this chapter agrees with their result. However, the transition to complementarity over time is entirely dependent upon the long-term mechanism of species coexistence, such that if species coexist by means other than resource partitioning, sampling effects should continue to dominate any biodiversity effects of more species-rich mixtures over time.

Biodiversity effects, niche theory, and patterns of extinction

In this chapter I have presented three different modeling techniques to estimate the effects of diversity on species mixture yields and how those effects should change along resource gradients. The phenomenological plant competition model (Eq. 1) reveals how interaction coefficients can be used to describe different mechanistic relationships between species diversity and productivity. The resource-based competition model further describes the sensitivity of the main two mechanisms, complementarity and sampling effects, to different levels of resource supply, and how the occurrence of these processes depends on levels of resource partitioning and relative carrying capacities (monoculture yields). Finally, the dynamic Lotka-Volterra model with intermediate disturbance frequencies suggests that non-equilibrium mechanisms of species coexistence also lead to positive biodiversity effects, but only by means of sampling effects that increase with resource levels (if resource enrichment increases the rate of competitive displacement). All three models suggest that resource partitioning begets complementarity and dominance begets sampling effects.

Thus, for all scenarios, the full range of biodiversity effects for any species assemblage can be predicted from only two species characteristics: 1) species resource requirements, which determine whether species may partition resources, thus establishing the existence of complementarity; and 2) species resource consumption rates, which determine monoculture yields (carrying capacities) and thus the potential intensity of sampling effects. The relative equilibrium competitive abilities for a group of species at a given resource level are determined by both minimum resource requirements (e.g., R*) and by consumption rates (consumption vectors). In other words, because complementarity effects depend on resource partitioning, species resource requirements should determine the potential CE of a species assemblage; because sampling effects depend on dominance relationships, relative consumption rates should determine the potential SE of a species assemblage. Together, knowledge of these two species characteristics should allow reasonable predictions of how a particular species assemblage might influence ecosystem processes compared to its compositional subsets (again, ignoring higher-order interactions).

The distinction between environmental requirements of species versus their per-capita impact on the environment is a common if often implicit contrast in community ecology. It is perhaps the very basis of the different definitions of "niche" that have been introduced since the concept was first defined by Grinnell and Elton in the 1910s and 20s. Indeed, this distinction describes the unique aspects of the Grinnellian and Eltonian definitions in the first place: Grinnell (1917) first described niches of organisms with particular reference to their environmental requirements (see also Shelford 1913), while Elton (1927) based his ecological niche on the impact of a species on its ecosystem,

especially its trophic role (see Leibold 1995). Since then, nearly every reformulation of the niche has chosen to refine one or both of these aspects, whether from the Grinnellian side (e.g., Andrewartha and Birch's "ecological web" (1954); Hutchinson's "fundamental niche" (1957); Whittaker et al.'s "habitat" (1973); Leibold's "requirement niche") or the Eltonian side (MacArthur and Levins' resource consumption model (1967); Whittaker et al.'s "niche" (1973); Leibold's "impact niche" (1995)), to name but a few; see reviews in Schoener (1989), Colwell (1992), and Leibold (1995).

The environmental requirements versus impacts distinction is ubiquitous in ecology, even in far more specific treatments of particular ecological and evolutionary relationships. For example, Goldberg (1990) formulated a whole theory of plant competition around two separable aspects of species interaction: "competitive response", or ability of species to tolerate low levels of a particular resource, and "competitive effect", or the rate at which species consume a particular resource. Clearly, competitive response concerns resource requirements (akin to R*), while competitive effect concerns impacts of species on their environment (akin to consumption rates). (Indeed, this distinction potentially resolves several rather contentious debates concerning the nature of plant competition; see Grace 1990). Similarly, Antonovics (1978) made the distinction of range of resource utilization versus utilization efficiency of existing resources among pasture plant genotypes; Aarssen (1983) extended this reasoning to natural selection, suggesting that, when faced with a common competitor, species may either undergo character displacement (separation in niche space or "ecological combining ability"), or evolution may favor changes related to the rate of resource exploitation, making a species a better competitor ("competitive combining ability").

This dual niche concept was connected explicitly to mechanistic models of species coexistence by Leibold (1995), whose reasoning I will, in turn, use to connect the dual niche concept to both phenomenological and mechanistic models of the diversity-productivity relationship. Leibold used the basic MacArthur-Tilman resource ratio model to demonstrate how each part of the niche concept was reflected in the conditions necessary for species coexistence. In short, Leibold pointed out that species "requirement niches", corresponding to the resource requirements of species in the model (uniquely described by their ZNGIs, as defined above), determine whether a suite of species can *possibly* coexist at equilibrium (following MacArthur 1972 and Tilman 1982). That is, species must somehow partition resources to coexist, as discussed above. But to determine whether such coexistence is stable, one has to consider species "impact niches", or the vector sum rate at which species consume resources. As discussed above, stability occurs if species limit their own growth more than they are limited by other species. So realized diversity levels (at equilibrium) are dependent upon both aspects of the dual niche concept.

In an entirely analogous manner, the extent to which species diversity influences productivity depends upon the requirement and impact niches of the species involved. Biodiversity effects are the sum of complementarity and sampling effects. Complementarity effects emerge in biodiversity experiments (again, assuming equilibrium) if the two conditions for coexistence are met; that is, species partition resources and they consume relatively more of the resources that limit themselves. Sampling effects emerge in biodiversity experiments when species have high impact niches relative to other species, which leads to dominance. Dominance, in turn, causes

species mixtures to take on the properties of the dominant species, which can either enhance productivity above the average of its monoculture values or in some cases lead to negative biodiversity effects when dominate species have low carrying capacities. Away from equilibrium where species coexist because dominance relationships are never realized, the impact niche takes over as the principal determinant of biodiversity effects. Importantly, however, species mixtures can never be more productive than the most productive monoculture if complementarity does not occur; if this more stringent criterion must be met, it is the requirement niche that determines the diversity-productivity relationship.

The dependence of biodiversity effects on the two seemingly separable niche aspects of requirement versus impact niches begs the question as to whether these two niche dimensions are independent. Similar questions have been asked at larger scales in community ecology; for example, whether a species range size (perhaps indicating niche breadth, or a wide requirement niche) is related to its local abundance (perhaps an indication of the impact of species on its environment, though not on a per-capita basis) (Brown 1995, Gaston 1996, Hubbell 2001). But the question as posed here relates specifically to local interactions. For example, plant species differ in both their phenology (which may contribute to complementarity) and their mature sizes and growth rates (which may contribute to sampling effects), and there is little reason to believe that these traits are necessarily correlated. However, the finite nature of exploitable resources suggests an upper bound to the independence of complementary resource use and the rates at which species use resources—at some point, hoarding of resources by species of high dominance value will restrict complementary resource use, and vice-versa. To

explore this scenario theoretically, levels of species complementarity and dominance must be translated into one another, perhaps by expressing each in terms of a community resource (Schwartz et al. 2000). Indeed, the analysis of the relationship between CE and SE in a prior experiment (see Chapter 4) suggests that the potential for high dominance, leading to high sampling effects, tends to preclude significant complementarity in species mixtures.

Finally, the utility of the dual niche concept can be expanded to studies of the relationship between ecosystem functioning and levels of species extinction, more germane to the "maintenance" of ecosystem function perspective outlined in Chapter 1. A current major problem of simulation models that attempt to predict the effects of species extinction on ecosystem functioning is that species extinction is modeled as a random process (e.g., Tilman et al. 1997a, Naeem 1998, Nijs and Impens 2000, Petchey 2000). This is inherently problematic because neither historical nor current extinction patterns are random (Raup 1994, Kerr and Currie 1995, Bennett and Owens 1997, Gaston and Blackburn 1997, McKinney 1997, Purvis et al. 2000b). The dual niche concept provides a possible solution to this problem because it gives researchers a basis for including deterministic extinction patterns by having species go extinct according to their "impact niche" values, which may have real analogues in natural extinction processes. For example, what if species that individually had the lowest per-capita impact on their environment were to go extinct first? This may occur if impact values were related to abundance and the rarest, least-functional species suffer the greatest extinction risk (MacArthur and Wilson 1967, Lande 1998). At the other extreme, species may go extinct in the order of highest to lowest impact values. This may occur, for example, if

large, keystone species that require the largest home ranges or were the poorest dispersers were most susceptible to extinction from habitat loss (Tilman and Lehman 1997). Intuitively, if species of higher per-capita environmental impacts suffer higher extinction risk, ecosystem functioning should be far more sensitive to species loss than if species extinction is a random process. The coupling of real extinction patterns to studies of how the functioning of ecosystems responds to extinctions should be a research priority (Bond 1994, Nijs and Impens 2000).

Conclusion

The modeling techniques presented in this chapter were meant to overcome several limitations of the prevailing theoretical treatments of diversity-productivity relationships. In particular, these techniques allowed predictions of how resource availability should influence complementarity and sampling effects (and thus total diversity effects) and how mechanisms of species coexistence relate to those of diversity effects. A plant competition model incorporating a "community matrix" revealed how the nature of pairwise species interactions could be used to predict diversity-productivity relationships, and demonstrated that competition, complementarity, and facilitation could be detected and defined based on pairwise species interaction coefficients (alphas). When explicit competition for resources was added to this framework using the MacArthur-Tilman resource ratio model, I demonstrated that biodiversity effects (at least for a two-species mixture) were highly dependent upon resource supply points. Sampling effects increase with resource enrichment due to higher dominance levels, while complementarity depends on whether a particular resource supply position contributes to

species coexistence. Away from equilibrium, when species coexist due to intermediate disturbance levels, sampling effects based on species dominance dictate increased biodiversity effects along a resource (displacement rate) gradient. Finally, I showed how complementarity and sampling effects, the two principal mechanisms of the biodiversity effects, are yet another manifestation of the dual niche concept of requirement versus impact niches.

In general, there was relatively little agreement between previous experimental results (described in Chapters 3 and 4) and the theory presented in this chapter, particularly concerning the sensitivity of sampling effects to resource enrichment. It is important to note, however, that the two experiments were not formulated as tests of the theory in this chapter, but of the theory described in Chapter 2 relating to habitat selection versus competitive dominance, and indeed the experimental results are more consistent with the latter. Many of the inconsistencies between this theory and the experimental results can be explained by the use of a mostly annual species pool in the experiments. In particular, dominance relationships, which couple resource enrichment to greater sampling effects, would not be expected to be fully realized after one growing season using ruderal species. The theory presented in this chapter should be more applicable to perennial herb communities that have had enough time to establish complementary and dominance relationships. Although beyond the resources of this dissertation, many such studies are currently being performed around the world (e.g., Hector et al. 1999, Tilman et al. 2001).

Table 5.1. Suggested definitions of interspecific interactions based on the interaction coefficients (alphas) of two hypothetical species A and B. Details are given in the text.

	$\alpha_{AB} < 0$	$0 < \alpha_{AB} < 1$	$1 < \alpha_{AB}$
$\alpha_{BA} < 0$	reciprocal facilitation	facilitation	unknown (?)
$0 < \alpha_{BA} < 1$	facilitation	complementarity	exploitation competition
$1 < \alpha_{BA}$	unknown (?)	exploitation competition	interference competition

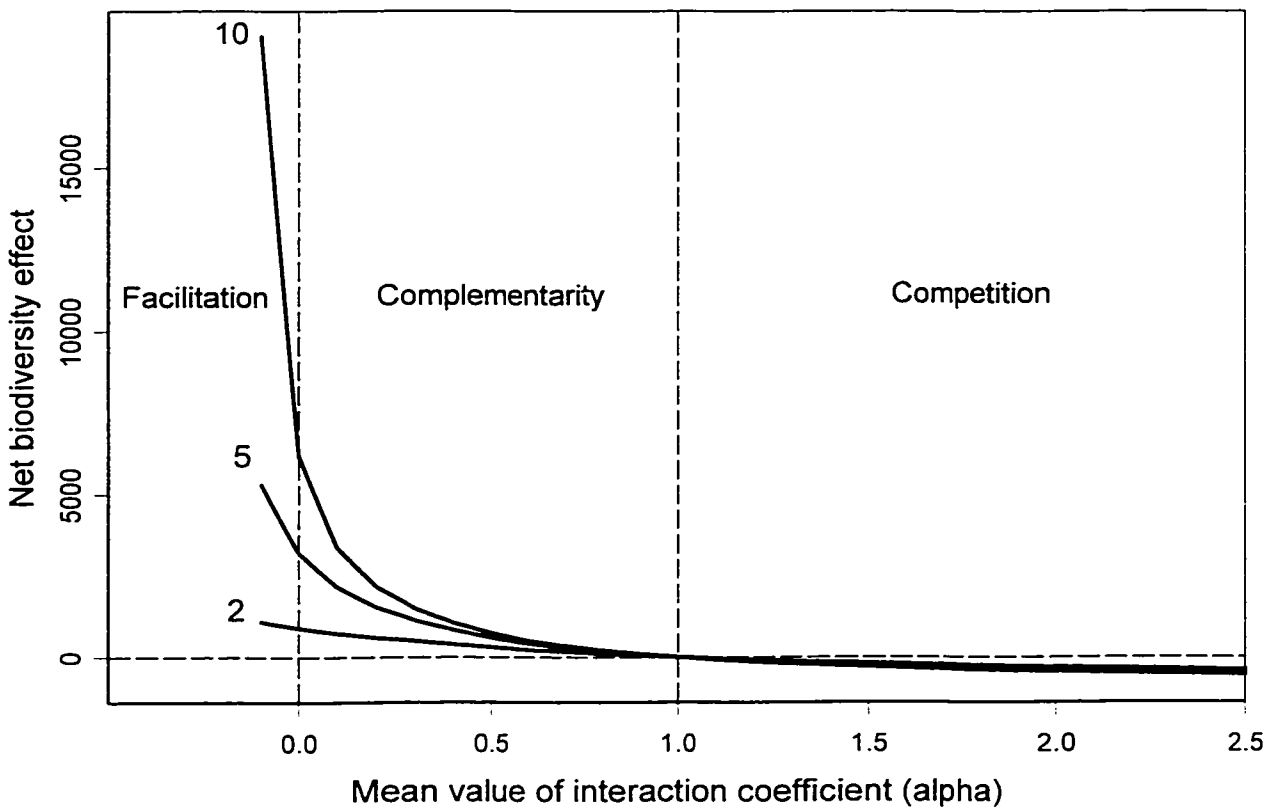

Figure 5.1. The relationship between mean alpha value of the community matrix and the net biodiversity effect of the mixture (defined as the difference between the expected mixture yield, based on monoculture values, and the observed mixture yield) for mixtures of 10, 5, and 2 species. Parameter values for model (1) were: $\overline{w}_{m,i} = 50$, $a = 0.05$, total $N = 500$.

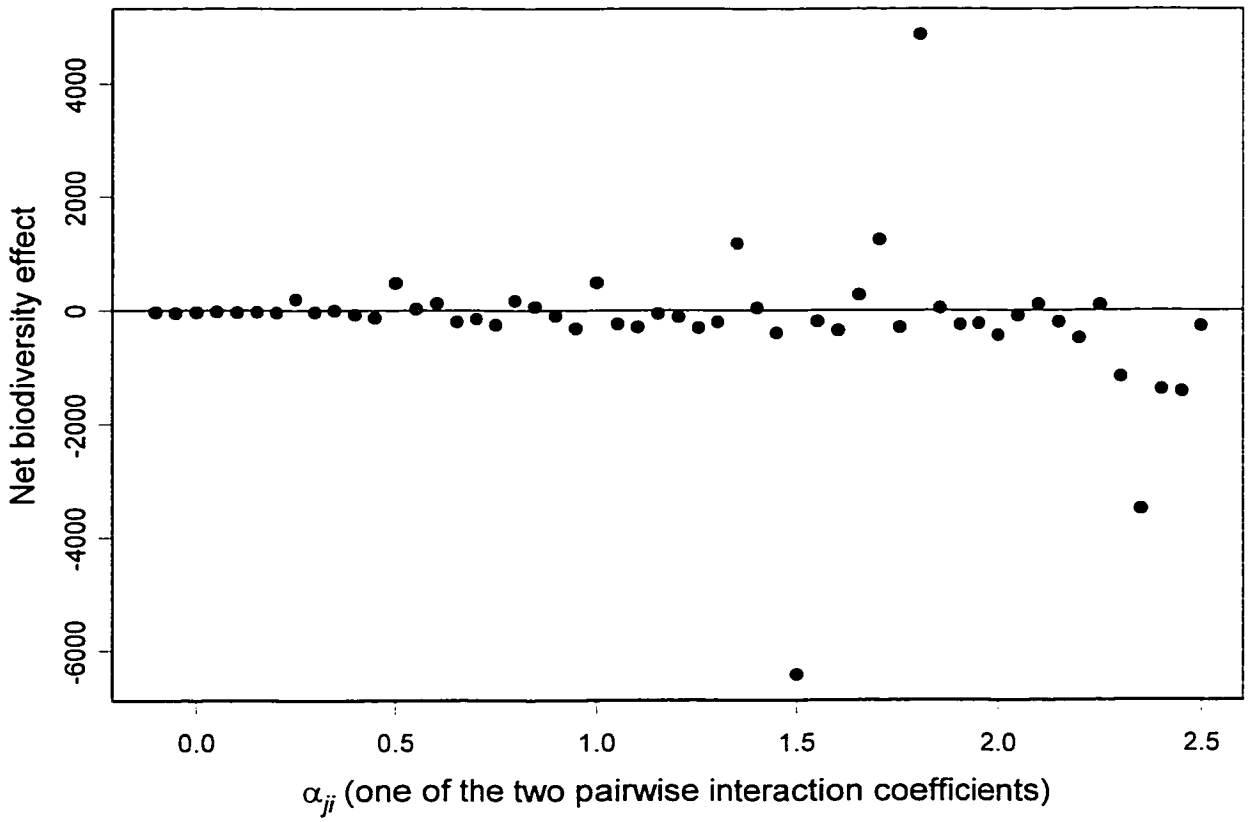

Figure 5.2. The effect of a reciprocal competitive relationship on the biodiversity effect of two species of the same monoculture value in a simulated "biodiversity" experiment. The ordinate is the net biodiversity effect from Figure 5.1. The abscissa is one of the pairwise alphas (effect of species *j* on species *i*); the other alpha is the reciprocal of the first ($\alpha_{ji} = 1/\alpha_{ij}$), with normally distributed error of mean $1/\alpha_{ij}$ and standard deviation of ($.1/|\alpha_{ji}|$). Parameter values are listed in Figure 5.1.

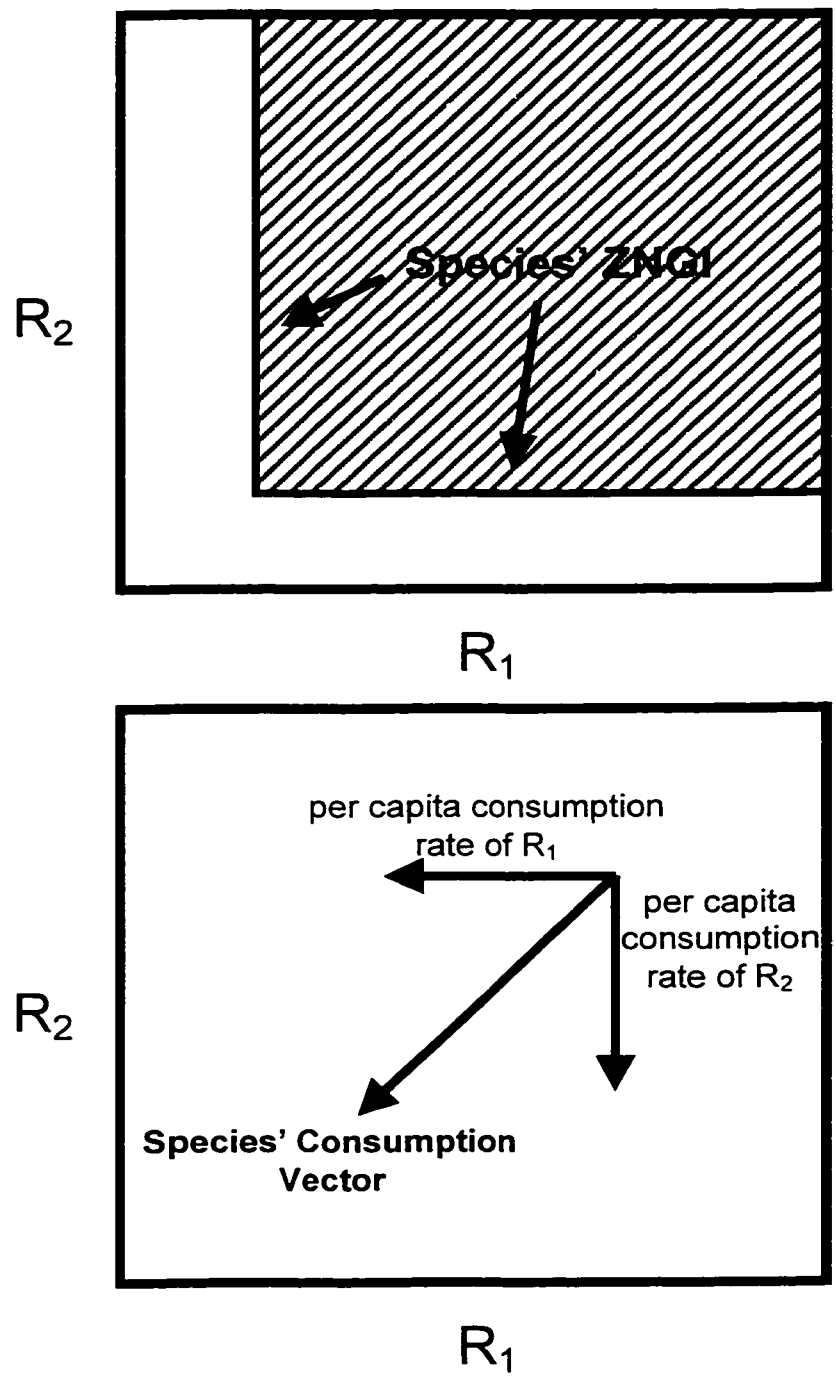

Figure 5.3. The two major species traits of the resource ratio competition model (MacArthur 1972, Tilman 1982). Both figures are phase-planes of the concentrations of two resources. The upper figure shows a "zero-net growth isocline" (ZNGI) for essential resources where a species has a positive per capita growth rate in the shaded area. The lower figure illustrates a "consumption vector" or the vector sum of the rate at which a species consumes resources 1 and 2.

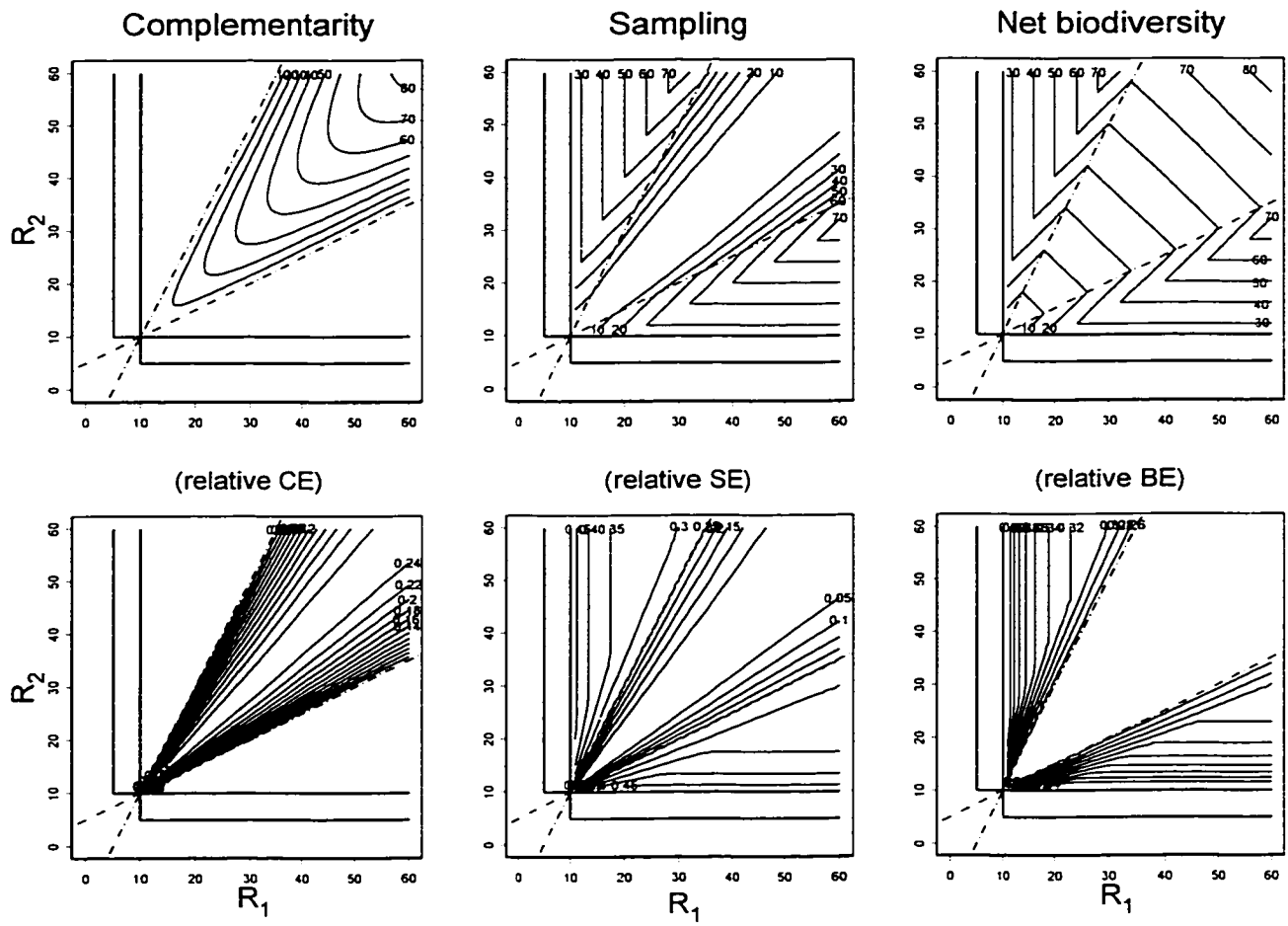

Figure 5.4. Contour graphs of complementarity, sampling, and net biodiversity effects for a two-species resource competition model meeting the conditions of stable coexistence, where zero-net growth isoclines (ZNGIs) overlap and each species consumes relatively more of the resource that limits itself. Axes are levels of each resource, bold lines are ZNGIs, dotted-dashed lines are consumption vectors, and contour lines represent the level of the corresponding biodiversity effect component for a resource supply point. Bottom graphs divide CE, SE, and BE values by the total mixture yield. Parameter values are given in Appendix B.

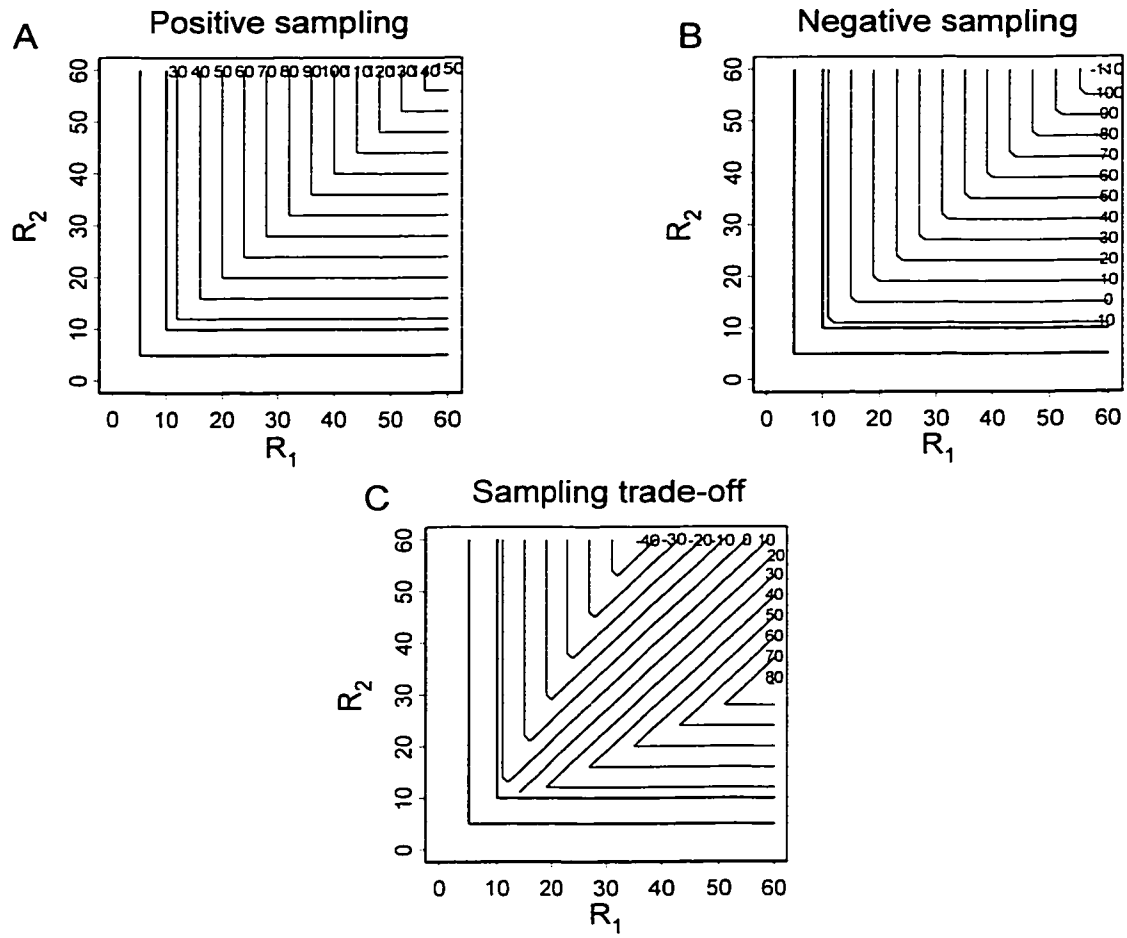

Figure 5.5. Contour graphs of sampling effects for a two-species resource competition model where one species "wins". A) The wining species has a higher carrying capacity; B) the wining species has a lower carrying capacity; C) relative carrying capacity of the winning species depends upon resource supply. Graph features are the same as Figure 5.4.

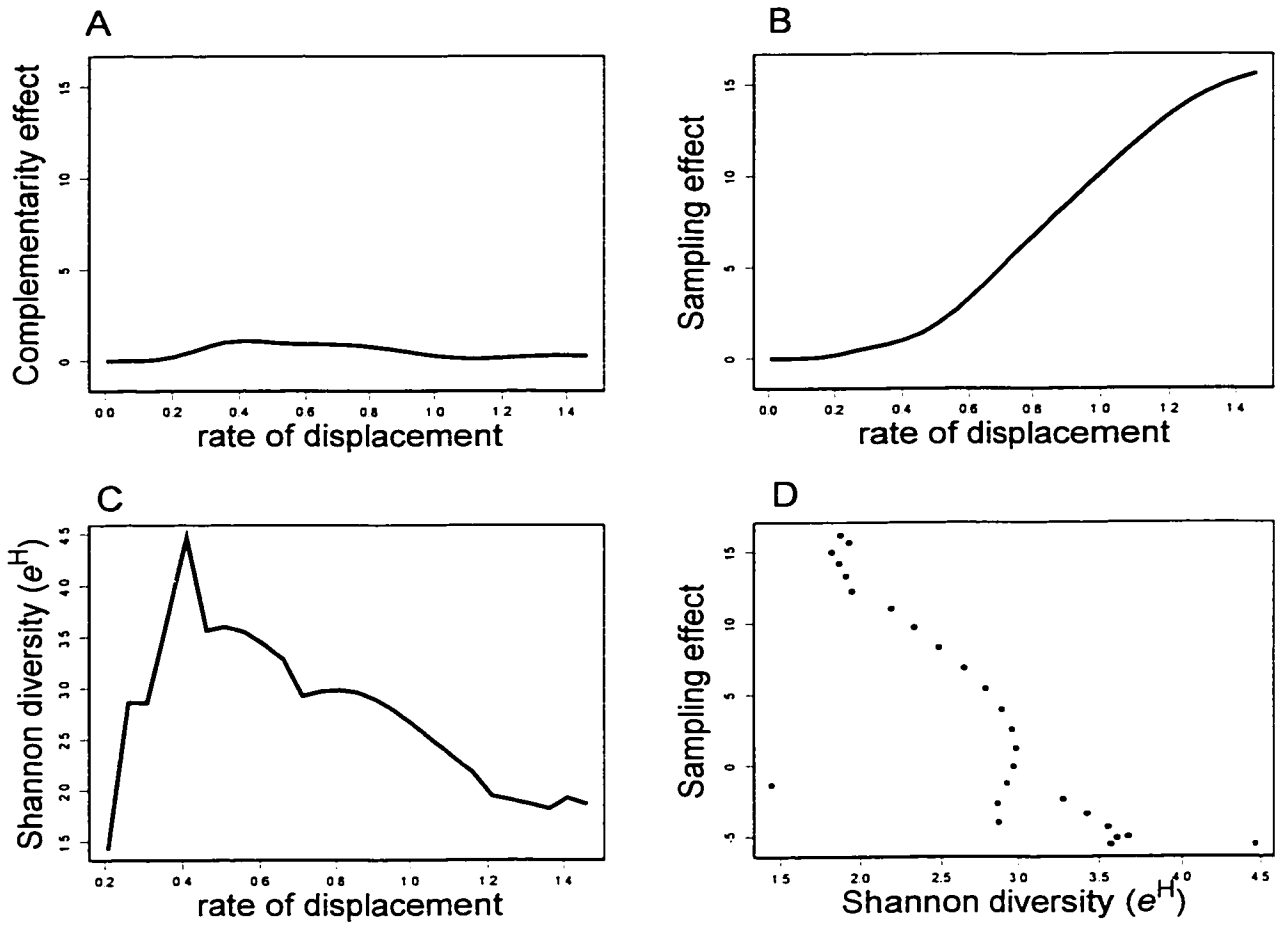

Figure 5.6. Predicted biodiversity effects on yield along a rate of competitive displacement gradient in a dynamic Lotka-Volterra competition model with intermediate disturbance frequency and no resource partitioning. Graphs A and B show calculated complementarity (CE) and sampling effects (SE) along the displacement gradient; graph C shows how species diversity depends upon the displacement rate at intermediate disturbance levels (Huston 1979). Graph D demonstrates the relationship between dominance and SE. Parameter values for simulations are listed in Appendix B.

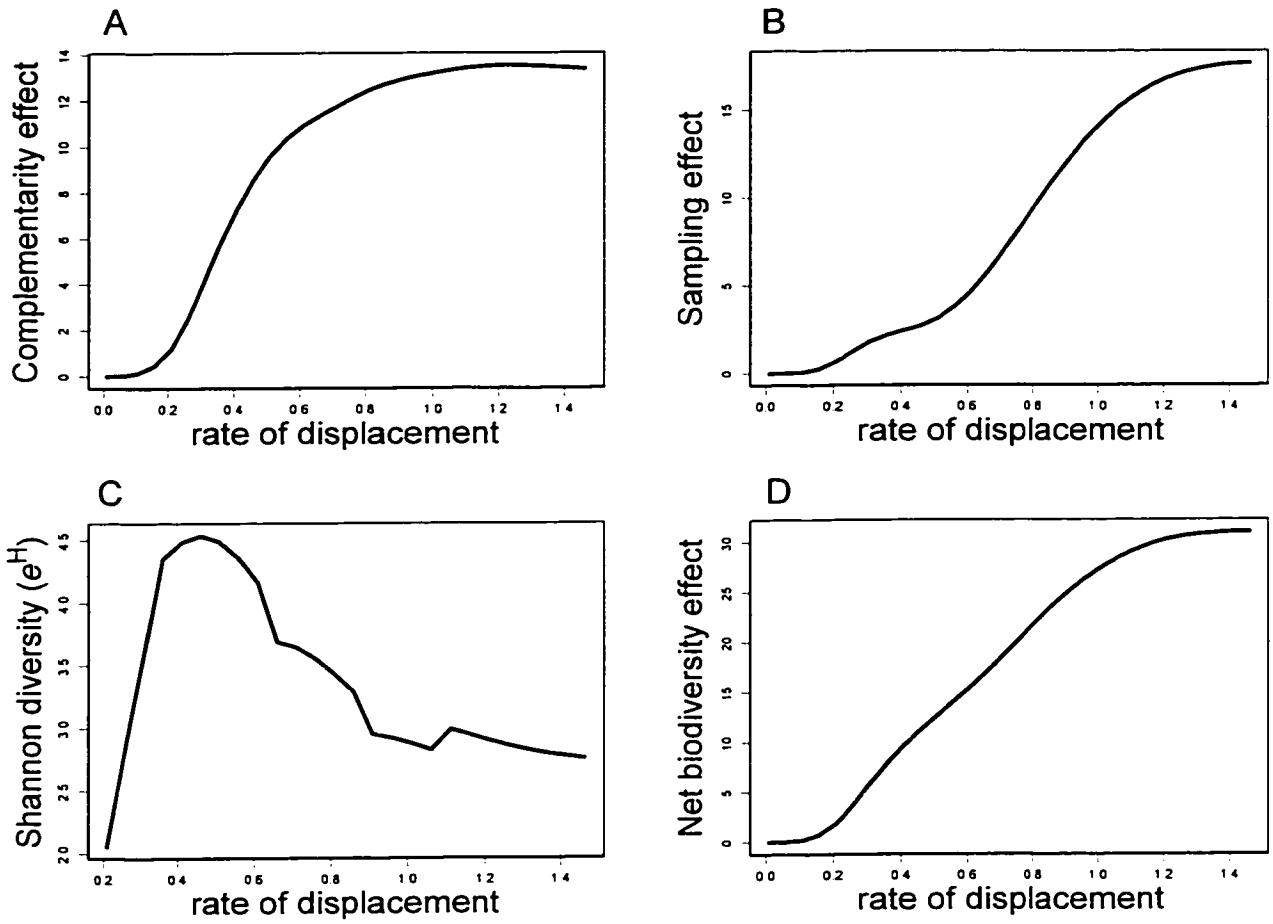

Figure 5.7. Complementarity, sampling, and net biodiversity effects for a non-equilibrium Lotka-Volterra model of six-species competition where species partition resources (all $\alpha_{ij} = 0.5$; all $\alpha_{ii} = 1$). All other parameters are the same as those illustrated in Figure 5.6. Graph C shows the relationship between competitive displacement rate and species diversity.

APPENDIX A:

Analytical solution of the "cancellation effect" of competition and complementarity in the hyperbolic competition model

In two species competition when monoculture values are equal, positive biodiversity effects occur solely as the result of net complementarity, where the relative yields of species sum to more than 1; negative biodiversity effects occur as the result of net competition, where relative yields sum to less than 1. Effects of complementarity and competition perfectly "cancel" each other when the sum of relative yields equals 1:

$$RY_i + RY_j = 1$$

Or, equivalently in the Loreau and Hector (2001) additive partition, when the deviation of observed and expected relative yields cancel each other:

$$\Delta RY_i = - \Delta RY_j$$

Which can also be expressed as the sum of mixture yields (P) equaling the monoculture yield (M):

$$P_i + P_j = M$$

In terms of the hyperbolic competition model (Equation 1, Chapter 5), this translates to:

$$\frac{Nw}{1 + a\,(N + \alpha N)} + \frac{Nw}{1 + a\,(N + \beta N)} = \frac{2Nw}{1 + 2aN}$$

where N is the mixture sowing density per species, w is the mature size of an isolated individual, a describes the intensity of intraspecific competition, and α and β are the interspecific coefficients that describe the pairwise interactions between the two species. If N, w, and a are equal for both species, this simplifies to:

$$\frac{1}{1+a(N+\alpha N)}+\frac{1}{1+a(N+\beta N)}=\frac{2}{1+2aN}$$

Solving for α:

$$\alpha=\frac{2+\frac{2}{aN}-\frac{\beta}{aN}}{2\beta+\frac{1}{aN}}$$

This is the analytical solution to the exact "cancellation effect" of competition and complementarity in the hyperbolic competition model. It is sensitive to both a and N, because density and intraspecific competition both affect the influences of the interaction coefficients in the model. When monoculture yields are equal, it is not sensitive to the size of each species.

Figure 6.1 illustrates the relationship between the above analytical solution of the cancellation effects and an exact reciprocal relationship between the pairwise interaction coefficients (α=1/β) where N=250 and a=1/1000. Over the range of coefficients that probably describes most plant interactions, the deviation between these two functions is small.

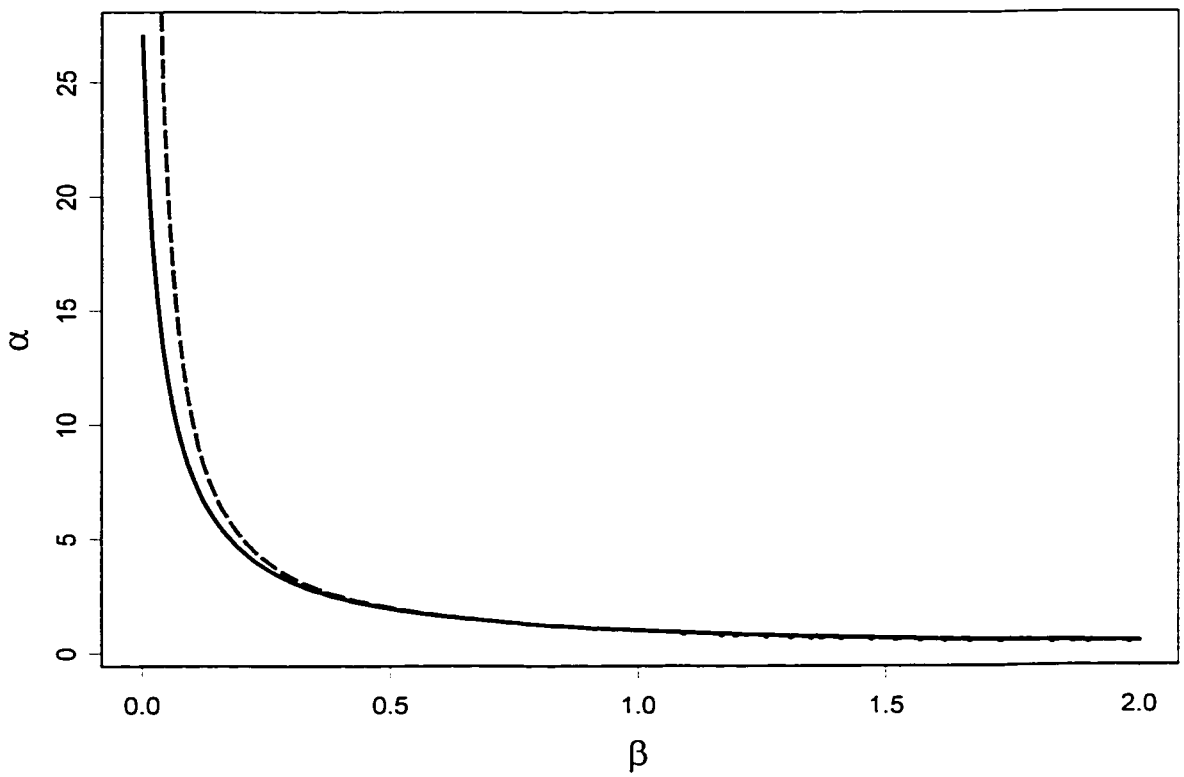

Figure 6.1. The actual relationship between pairwise competition coefficients that produces a "cancellation effect" of competition and complementarity (sold line), versus the true reciprocal relationship ($\alpha=1/\beta$) (dashed line). The deviation between these two relationships is zero when either coefficient is 1 and increases away from 1 in both directions. Within the typical range of plant interactions (say, 0.5 and 2), the deviation is minimal. For the above curves, N=250 and a=1/1000.

APPENDIX B:

Equations and parameters of simulations

in chapter 5

Parameters and analytical solution of the resource ratio model

Follwing Tilman (1982), mixture densities (yields) were calculated for species 1 and 2 as:

$$N_1 = \frac{K_1 - \frac{c_{11}}{c_{21}} K_2}{1 - \frac{c_{11}c_{22}}{c_{21}c_{12}}} \qquad N_2 = \frac{K_2 - \frac{c_{22}}{c_{12}} K_1}{1 - \frac{c_{11}c_{22}}{c_{21}c_{12}}}$$

K_i is the carrying capacity (monoculture yield) of species i:

$$K_i = \mathrm{MIN}_j[(S_j - R^*_{ij})(a/c_{ij})]$$

c_{ij} is the consumption rate of species i for resource j,

S_j is the supply level for resource j,

R^*_{ij} is the level of resource j below which species i has negative net growth, and

a is a resource supply constant.

Note that mortality rate is not needed when R^* is specified.

For all the simulations in Chapter 5, I used the following parameter values: $a = 1$; S ranged from 11 to 60 for each resource; c values were .1 and .2, depending on the simulation, and R^* values were 5 and 10, depending on the simulation.

Parameters of the dynamic Lotka-Volterra model

The following parameters were used for six-species competition:

Carrying capacities (K) = {60, 50, 40, 30, 20, 15}

Growth rates (r) = *rconstant* * {0.1, 0.25, 0.3, 0.4, 0.5, 0.6}; *rconstant* is the varied rate of competitive displacement (0.01 to 1.50, 0.05 increments)

Total time steps = 40

Disturbance frequency = 14 (number of time steps between disturbances)

Disturbance magnitude = 0.83 (proportion of density lost of each species at each disturbance)

Competition coefficients in scenario 1 all equal 1; for scenario 2 all interspecific coefficients were changed to 0.5.

REFERENCES

Aarssen, L.W. 1983. Ecological combining ability and competitive combining ability in plants: toward a general evolutionary theory of coexistence in systems of competition. American Naturalist 122: 707-731.

Aarssen, L.W. 1997. High productivity in grassland ecosystems: effected by species diversity or productive species? Oikos 80: 183-184.

Allen, L.H., Sinclair, T.R. and Lemon, E.R. 1976. Radiation and microclimate relationships in multiple cropping systems. In: Papendick, R.I., Sanchez, P.A. and Triplett, G.B. (eds), Multiple cropping. American Society of Agronomy, Madison, WI, pp. 171-200.

Al-Mufti, M.M., Sydes, C.L., Furness, S.B., Grime, J.P., Band, S.R. 1977. A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. Journal of Ecology 65:759-791.

Altieri, M.A. 1999. The ecological role of biodiversity in agroecosystems. Agriculture Ecosystems & Environment 74: 19-31.

Andow, D.A. 1991. Vegetational diversity and arthropod population response. Annual Reviews of Entomology 36: 561-586.

Andrewartha, H.G. and Birch, L.C. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, IL.

Antonovics, J. 1978. The population genetics of mixtures. In: Wilson, J.R. (Ed.), Plant relations in pastures. CSIRO, Melbourne, pp. 233-253.

Armstrong, R.A. and McGehee, R. 1980. Competitive exclusion. American Naturalist 115: 151-170.

Austin, M.P. 1999. The potential contribution of vegetation ecology to biodiversity research. Ecography 22: 465-484.

Austin, M.P. and Austin, B.O. 1980. Behaviour of experimental plant communities along a nutrient gradient. Journal of Ecology 68: 891-918.

Austin, M.P. and Smith, T.M. 1989. A new model for the continuum concept. Vegetatio 83: 35-47.

Austin, M.P., Fresco, L.F., Nicholls, A.O., Groves, R.H. and Kaye, P.E. 1988. Competition and relative yield estimation and interpretation at different densities and under various nutrient concentrations using *Silybum marianum* and *Cirsium vulgare*. Journal of Ecology 76: 157-171.

Ayala, F. 1968. Genotype, environment, and population numbers. Science 162: 1453-1459.

Bazzaz, F.A. 1996. Plants in changing environments: linking physiological, population, and community ecology. Cambridge University Press, Cambridge, U.K.

Bell, G. and Lechowicz, M.J. 1994. Spatial heterogeneity at small scales and how plants respond to it. In: Caldwell, M.M. and Pearcy, R.W. (eds.), Explotation of environmental heterogeneity by plants. Academic Press, New York, NY, pp. 391-414.

Bennett, P.M. and Owens, I.P.F. 1997. Variation in extinction risk among birds: chance or evolutionary predisposition? Proceedings of the Royal Society of London B 264: 401-408.

Bertness, M.D. and Callaway, R. 1994. Positive interactions in communities. Trends in Ecology and Evolution 9: 191-193.

Billick, I. and Case, T.J. 1994. Higher-order interactions in ecological communities: what are they and how can they be detected? Ecology 75: 1529-1543.

Bond, W.J. 1994. Keystone species. In: Schulze, E.-D. and Mooney, H.A. (eds.), Biodiversity and ecosystem function. Springer-Verlag, New York, NY, pp. 237-253.

Brown, J.H. 1995. Macroecology. Chicago University Press, Chicago, IL.

Brown, R.L. and Peet, R.K. Diversity and invasibility of Southern Appalachian plant communities. Ecology, in press.

Caldwell, M.M., Dawson, T.E. and Richards, J.H. 1998. Hydraulic lift: consequences of water efflux from the roots of plants. Oecologia 113: 151-161.

Callaway, R.M. 1995. Positive interactions among plants. Botanical Review 61: 306-349.

Callaway, R.M. and Walker, L.R. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78: 1958-1965.

Campbell, B.D. and Grime, J.P. 1992. An experimental test of plant strategy theory. Ecology 73: 15-29.

Case, T.J. and Bender, E.A. 1981. Testing for higher-order interactions. American Naturalist 118: 920-929.

Caswell, H. 1982. Life history theory and the equilibrium status of populations. American Naturalist 120: 317-339.

Chapin, F.S. 1980. The mineral nutrition of wild plants. Annual Review of Ecology and Systematics 11: 233-260.

Chesson, P.L. 1986. Environmental variation and the coexistence of species. In: Diamond, J. and Case, T.J. (eds), Community Ecology. Harper & Row, New York, NY, pp. 240-256.

Chesson, P.L. and Case, T.J. 1986. Nonequilibrium community theories: chance, variability, history, and coexistence. In: Diamond, J. and Case, T.J. (eds), Community Ecology. Harper & Row, New York, NY, pp. 229-239.

Clements, F.E., Weaver, J.E., and Hanson, H.C. 1929. Plant competition: an analysis of community functions. Carnegie Institute, Washington, D.C.

Colwell, R.K. 1992. Niche: a bifurcation in the conceptual lineage of the term. In: Fox-Keller, E. and Lloyd, E.A. (eds), Keywords in evolutionary biology. Harvard University Press, Cambridge, MA, pp. 241-248.

Colwell, R.K. and Futuyma, D.J. 1971. On the measurement of niche breadth and overlap. Ecology 52: 567-576.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302-1309.

Connell, J.H. and Lowman, M.D. 1989. Low-diversity tropical rain forests: some possible mechanisms for their existence. American Naturalist 134: 88-119.

Cornell, H.V. 1999. Unsaturation and regional influences on species richness in ecological communities: a review of the evidence. Ecoscience 6: 303-315.

Cornell, H.V. and Lawton, J.H. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. Journal of Animal Ecology 61: 1-12.

Council for Agricultural Science and Technology. 1999. Benefits of biodiversity. CAST, Ames, IA.

de Wit, C.T. 1960. On competition. Verslagen Landbouwkundige Onderzoekingen 66: 1-82.

de Wit, C.T. and van den Bergh, J.P. 1965. Competition between herbage plants. Netherlands Journal of Agricultural Science 13: 212-221.

de Wit, C.T., Tow, P.G., and Ennik, G.C. 1966. Competition between legumes and grasses. Verslagen Landbouwkundige Onderzoekingen 687: 3-30.

del Moral, R. and Wood, D.M. 1993. Early primary succession on a barren volcanic plain at Mount St. Helens, Washington. American Journal of Botany 80: 981-991.

Doak, D.F., Bigger, D., Harding, E.K., Marvier, M.A., O'Malley, R.E., and Thomson, D. 1998. The statistical inevitability of stability-diversity relationships in community ecology. American Naturalist 151: 264-276.

Ehrlich, P.R. and Ehrlich, A.H. 1981. Extinction: the causes and consequences of the disappearance of species. Ballantine Books, New York, NY.

Elton, C. 1927. Animal ecology. Sidgwick & Jackson, London, U.K.

Elton, C. 1958. The ecology of invasions by animals and plants. Methuen, London, U.K.

Endler, J.A. 1993. The color of light in forests and its implications. Ecological Monographs 63: 1-27.

Engelhardt, K.A.M and Ritchie, M.E. 2001. Effects of macrophyte species richness on wetland ecosystem functioning and services. Nature 411: 687-689.

Ernst, S.K.M. and Brown, J.H. 2001. Homeostasis and compensation: the role of species and resources in ecosystem stability. Ecology 82: 2118-2132.

Ewel, J.J. 1986. Designing agricultural ecosystems for the humid tropics. Annual Review of Ecology and Systematics 17: 245-271.

Ewers, B.E., Oren, R., and Sperry, J.S. 2000. Influence of nutrient versus water supply on hydraulic architecture and water balance in *Pinus taeda*. Plant Cell & Environment 23:1055-1066.

Firbank, L.G. and Watkinson, A.R. 1985. A model of interference within plant populations. Journal of Theoretical Biology 116: 291-311.

Firbank, L.G. and Watkinson, A.R. 1986. Modelling the population dynamics of an arable weed and its effects upon crop yield. Journal of Applied Ecology 23: 147-159.

Fowler, N. 1986. The role of competition in plant communities in arid and semiarid regions. Annual Review of Ecology and Systematics 17: 89-110.

Freckleton, R.P. and Watkinson, A.R. 1997. Measuring plant neighbor effects. Functional Ecology 11: 532-536.

Freckleton, R.P. and Watkinson, A.R. 2000. Designs for greenhouse studies of interactions between plants: an analytical perspective. Journal of Ecology 88: 386-391.

Freckleton, R.P. and Watkinson, A.R. 2001. Predicting competition coefficients for plant mixtures: reciprocity, transitivity and correlations with life-history traits. Ecology Letters 4: 348-357.

Fridley, J.D. 2001. The influence of species diversity on ecosystem productivity: how, where, and why? Oikos 93:514-526.

Frost, T.M., Carpenter, S.R., Ives, A.R., and Kratz, T.K. 1995. Species compensation and complementarity in ecosystem function. In: Jones, C.D. and Lawton, J.H. (eds), Linking species and ecosystems. Chapman & Hall, New York, NY, pp. 224-239.

Garnier, E., Navas, M.-L., Austin, M.P., Lilley, J.M. and Gifford, R.M. 1997. A problem for biodiversity-productivity studies: how to compare the productivity of multispecific plant mixtures to that of monocultures? Acta Oecologia 18: 657-670.

Gaston, K.J. 1996. Biodiversity: a biology of numbers and difference. Oxford University Press, Cambridge, MA.

Gaston, K.J. and Blackburn, T.M. 1997. Evolutionary age and risk of extinction in the global avifauna. Evolutionary Ecology 11: 557-565.

Gauss, G.F. 1934. The struggle for existence. Williams and Williams, Baltimore, MA.

Goldberg, D.E. and Miller, T.E. 1990. Effects of different resource additions on species diversity in an annual plant community. Ecology 71:213-225.

Goldberg, D.E. 1990. Components of resource competition in plant communities. In: Grace, J.B. and Tilman, D. (eds), Perspectives on plant competition. Academic Press, New York, NY, pp. 27-50.

Gough, L., Osenberg, C.W., Gross, K.L., and Collins, S.L. 2000. Fertilization effects on species density and primary productivity in herbaceous plant communities. Oikos 89:428-439.

Grace, J.B. 1990. On the relationship between plant traits and competitive ability. In: Grace, J.B. and Tilman, D. (eds), Perspectives on plant competition. Academic Press, New York, NY, pp. 51-65.

Grace, J.B. 1999. The factors controlling species density in herbaceous plant communities: an assessment. Perspectives in Plant Ecology, Evolution and Systematics 2: 1-28.

Griffiths, B.S., Ritz, K., Bardgett, R.D., Cook, R., Christensen, S., Ekelund, F., Sørensen, S.J., Bååth, E., Bloem, J., de Ruiter, P.C., Dolfing, J., and Nicolardot, B. 2000. Ecosystem response of pasture soil communities to fumigation-induced microbial diversity reductions: an examination of the biodiversity-ecosystem function relationship. Oikos 90:279-294.

Grime, J.P. 1973. Control of species density in herbaceous vegetation. Journal of Environmental Management 1: 151-167.

Grime, J.P. 1974. Vegetation classification by reference to strategies. Nature 250: 26-31.

Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist 111: 1169-1194.

Grime, J.P. 1979. Plant strategies and vegetation processes. John Wiley & Sons, London, U.K.

Grime, J.P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. Journal of Ecology 86: 902-910.

Grime, J.P. 2001. Plant strategies, vegetation processes, and ecosystem properties. Second edition. Wiley & Sons, New York, NY.

Grinnell, J. 1917. The niche-relationships of the California thrasher. Auk 34: 427-433.

Grubb, P.J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. Biological Reviews of the Cambridge Philosophical Society 52: 107-145.

Hairston, N.G., Allan, J.D., Colwell, R.K., Futuyma, D.J., Howell, J., Lubin, M.D., Mathias, J., and Vandermeer, J.H. 1968. The relationship between species diversity and stability: an experimental approach with protozoa and bacteria. Ecology 49: 1091-1101.

Halle, F. and Oldeman, R.A.A. 1975. An essay on the architecture and dynamics of growth of tropical trees. Penerbit Universiti Malaya, Kuala Lumpur, Malaysia.

Harper, J.L. 1977. Population biology of plants. Academic Press, New York, NY.

Hastings, A. 1997. Population biology: concepts and models. Springer-Verlag, New York, NY.

Hector, A. 1998. The effect of diversity on productivity: detecting the role of species complementarity. Oikos 82:597-599.

Hector, A. 2000. Developments in biodiversity and ecosystem functioning. Progress in Environmental Science 2: 155-162.

Hector, A. and Hooper, R. 2002. Darwin and the first ecological experiment. Science 295: 639-640.

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, J., Freitas, H., Giller, P.S., Good, J., Harris, R., Högberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Körner, C., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G., Otway, S.J., Pereira, J.S., Prinz, A., Read, D.J., Scherer-Lorenzen, M., Schulze, E.-D., Siamantziouras, A.S.D., Spehn, E., Terry, A.C., Troumbis, A.Y., Woodward, F.I., Yachi, S., and Lawton, J.H. 1999. Plant diversity and productivity experiments in European grasslands. Science 286:1123-1127.

Hodgson, J.G., Thompson, K., Wilson, P.J. and Bogaard, A. 1998. Does biodiversity determine ecosystem function? The Ecotron experiment reconsidered. Functional Ecology 12: 843-848.

Hooper, D.U. 1998. The role of complementarity and competition in ecosystem responses to variation in plant diversity. Ecology 79:704-719.

Hooper, D.U. and Vitousek, P.M. 1997. The effects of plant composition and diversity on ecosystem processes. Science 277: 1302-1305.

Hooper, D.U. and Vitousek, P.M. 1998. Effects of plant composition and diversity on nutrient cycling. Ecological Monographs 68:121-149.

Hubbell, S.P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, NJ.

Hughes, J.B. and Roughgarden, J. 2000. Species diversity and biomass stability. American Naturalist 155: 618-627.

Huston, M.A. 1979. A general hypothesis of species diversity. American Naturalist 113: 81-102.

Huston, M.A. 1993. Biological diversity, soils, and economics. Science 262: 1676-1680.

Huston, M.A. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, Cambridge, U.K.

Huston, M.A. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. Oecologia 110:449-460.

Huston, M.A. 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. Oikos 86: 393-401.

Huston, M.A. and DeAngelis, D. 1994. Competition and coexistence: the effects of resource transport and supply rates. American Naturalist 144: 854-877.

Huston, M.A., Aarssen, L.W., Austin, M.P., Cade, B.S., Fridley, J.D., Garnier, E., Grime, J.P., Hodgson, J., Lauenroth, W.K., Thompson, K., Vandermeer, J.H., and Wardle, D.A. 2000. No consistent effect of plant diversity on productivity. Science 289: 1255.

Hutchinson, G.E. 1957. Concluding remarks. Cold Spring Harbor Symposium on Quantitative Biology 22: 415-457.

Hutchinson, G.E. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? American Naturalist 93: 145-159.

Hutchinson, G.E. 1961. The paradox of the plankton. American Naturalist 95: 137-145.

Johnson, K.H., Vogt, K.A., Clark, H.J., Schmitz, O.J., and Vogt, D.J. 1996. Biodiversity and the productivity and stability of ecosystems. Trends in Ecology and Evolution 11: 272-277.

Jolliffe, P. 1997. Are mixed populations of species more productive than pure stands? Oikos 80: 595-602.

Kaiser, J. 2000. Rift of biodiversity divides ecologists. Science 289: 1282-1283.

Kartesz, J.T. 1994. A synonymized checklist of the vascular flora of the United States, Canada, and Greenland. Second Edition. Timber Press, Portland, OR.

Kerr, J.T. and Currie, D.J. 1995. Effects of human activity on global extinction risk. Conservation Biology 9: 1528-1538.

Kershaw, K.A. 1973. Quantitative and dynamic plant ecology. Elsevier, New York, NY.

Kinzig, A.P., Pacala, S.W., and Tilman, D. (eds) 2002. The functional consequences of biodiversity: empirical progress and theoretical extensions. Princeton University Press, Princeton, NJ.

Kirchner, T.B. 1977. The effects of resource enrichment on the diversity of plants and arthropods in a shortgrass prairie. Ecology 58:1334-1344.

Klug, J.L., Fischer, J.M., Ives, A.R., and Dennis, B. 2000. Compensatory dynamics in planktonic community responses to pH perturbations. Ecology 81:387-398.

Lambers, H., Camridge, M.L., Konings, H. and Pons, T.L. (eds.) 1990. Causes and consequences of variation in growth rate and productivity of higher plants. SPB Academic Publishing, The Hague.

Lande, R. 1998. Antropogenic, ecological and genetic factors in extinction and conservation. Researches on Population Ecology 40: 259-269.

Lavorel, S., Prieur-Richard, A.H., and Grigulis, K. 1999. Invasibility and diversity of plant communities: from patterns to processes. Diversity and Distributions 5:41-49.

Law, R. and Watkinson, A.R. 1987. Response-surface analysis of two-species competition: an experiment on *Phleum arenarium* and *Vulpia fasciculata*. Journal of Ecology 75: 871-886.

Lawton, J.H and Brown, V.K. 1994. Redundancy in ecosystems. In: Schulze, E.-D. and Mooney, H.A. (eds) Biodiversity and ecosystem function. Springer-Verlag, New York, NY, pp. 255-270.

Leibold, M.A. 1995. The niche concept revisited: mechanistic models and community context. Ecology 76: 1371-1382.

Leps, J., Osbornová-Kosinová, J., and Rejmánek, M. 1982. Community stability, complexity and species life history strategies. Vegetatio 50:53-63.

Leps, J., Brown, V.K., Diaz Len, T.A., Gormsen, D., Hedlund, K., Kailová, J., Korthals, G.W., Mortimer, S.R., Rodriguez-Barreuco, C., Roy, J., Santa Regina, I., van Dijk, C., van der Putten, W.H. 2001. Separating the chance effect from other diversity effects in functioning of plant communities. Oikos 92:123-134.

Levine, J.M. and D'Antonio, C.M. 1999. Elton revisited: a review of evidence linking diversity and invasibility. Oikos 87: 15-26.

Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, NJ.

Lodge, D.M. 1993. Biological invasions: lessons for ecology. Trends in Ecology and Evolution 8: 133-137.

Lonsdale, W.M. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology 80: 1522-1536.

Loreau, M. 1998a. Biodiversity and ecosystem functioning: a mechanistic model. Proceedings of the National Academy of Sciences USA 95: 5632-5636.

Loreau, M. 1998b. Separating sampling and other effects in biodiversity experiments. Oikos 82: 600-602.

Loreau, M. 2000. Biodiversity and ecosystem functioning: recent theoretical advances. Oikos 91: 3-17.

Loreau, M. and Hector, A. 2001. Partitioning selection and complementarity in biodiversity experiments. Nature 412: 72-76.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D., and Wardle, D.A. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294: 804-808.

Loucks, O.L. 1970. Evolution of diversity, efficiency, and community stability. American Zoologist 10: 17-25.

Ludwig, W. 1950. Zur Theorie der Konkurrenz: die Annidation (Einnischung) als fünfter Evolutionsfaktor. Zool. Anz. Ergänzungsband zu Band 145: 516-537.

MacArthur, R.H. 1955. Fluctuations of animal populations and a measure of community stability. Ecology 36: 533-536.

MacArthur, R.H. 1970. Species-packing and competitive equilibrium for many species. Theoretical Population Biology 1: 1-11.

MacArthur, R.H. 1972. Geographical ecology: patterns in the distributions of species. Harper & Row, New York, NY.

MacArthur, R.H. and Levins, R. 1967. The limiting similarity, convergence and divergence of coexisting species. American Naturalist 101: 377-385.

MacArthur, R.H. and Wilson, E.O. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ.

Margalef, R. 1963. On certain unifying principles in ecology. American Naturalist 97: 357-374.

May, R.M. 1973. Stability and complexity in model ecosystems. Princeton University Press, Princeton, NJ.

May, R.M. and MacArthur, R.H. 1972. Niche overlap as a function of environmental variability. Proceedings of the National Academy of Sciences USA 69: 1109-1113.

McCune, B. and Mefford, M.J. 1999. PC-ORD. Multivariate analysis of ecological data, version 4. MjM Software Design, Gleneden Beach, OR.

McGrady-Steed, J., Harris, P.M., and Morin, P.J. 1997. Biodiversity regulates ecosystem predictability. Nature 390: 162-165.

McKinney, M.L. 1997. Extinction vulnerability and selectivity: combining ecological and paleontological views. Annual Review of Ecology and Systematics 28: 495-516.

McNaughton, S.J. 1977. Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. American Naturalist 111:515-525.

Miller, T.E. 1994. Direct and indirect species interactions in an early old-field plant community. American Naturalist 143: 1007-1025.

Mitchell, T.D. and Hulme, M. 1999. Predicting regional climate change: living with uncertainty. Progress in Physical Geography 23: 57-78.

Morgan, J.L., Campbell, J.M. and Malcolm, D.C. 1992. Nitrogen relations of mixed-species stands on oligotrophic soils. In: Cannell, M.G.R., Malcolm, D.C. and Robertson, P.A. (eds), The ecology of mixed-species stands of trees. Blackwell Scientific, Oxford, U.K., pp. 65-85.

Naeem, S. 1998. Species redundancy and ecosystem reliability. Conservation Biology 12:39-45.

Naeem, S. 2000. Reply to Wardle et al. Bulletin of the Ecological Society of America 81:241-246.

Naeem, S. and S. Li. 1997. Biodiversity enhances ecosystem reliability. Nature 390:507-509.

Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. and Woodfin, R.M. 1994. Declining biodiversity can alter the performance of ecosystems. Nature 368: 734-737.

Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. and Woodfin, R.M. 1995. Empirical evidence that declining species diversity may alter the performance of terrestrial ecosystems. Philosophical Transactions of the Royal Society of London B 347: 249-262.

Naeem, S., Hakansson, K., Lawton, J.H., Crawley, M.J. and Thompson, L.J. 1996. Biodiversity and plant productivity in a model assemblage of plant species. Oikos 76: 259-264.

Naeem, S., Tjossem, S.F., Byers, D., Bristow, C., and Li, S. 1999a. Plant neighborhood diversity and production. Ecoscience 6: 355-365.

Naeem, S., Chapin, F.S., Costanza, R., Ehrlich, P.R., Golley, F.B., Hooper, D.U., Lawton, J.H., O'Neill, R.V., Mooney, H.A., Sala, O.E., Symstad, A.J. and Tilman, D. 1999b. Biodiversity and ecosystem functioning: maintaining natural life support processes. Issues in Ecology 4, Ecological Society of America.

Newman, E.I. 1973. Competition and diversity in herbaceous vegetation. Nature 244: 310-311.

Nijs, I. and Impens, I. 2000. Biological diversity and probability of local extinction of ecosystems. Functional Ecology 14: 46-54.

Pacala, S.W. and Silander, J.A. 1990. Tests of neighbourhood population dynamic models in field communities of two annual weed species. Ecological Monographs 60: 113-134.

Pacala, S.W. and Tilman, D. 1994. Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. American Naturalist 143: 222-257.

Pacala, S.W. and Tilman, D. 2002. The transition from sampling to complementarity. In: Kinzig, A.P., Pacala, S.W. and Tilman, D. (eds), The functional consequences of biodiversity. Princeton University Press, Princeton, NJ, pp. 151-166.

Parker, G.G. 1995. Structure and microclimate of forest canopies. In: Lowman, M.D. and Nadkarni, N.M. (eds), Forest canopies. Academic Press, New York, NY, pp. 73-106.

Pärtel, M., Zobel, M., Zobel, K., and van der Maarel, E. 1996. The species pool and its relation to species richness: evidence from Estonian plant communities. Oikos 75: 111-117.

Peet, R.K. 1992. Community structure and ecosystem function. In: Glenn-Lewin, D.C., Peet, R.K. and Veblen, T.T. (eds), Plant succession: theory and prediction. Chapman & Hall, New York, NY, pp. 103-151.

Petchey, O.L. 2000. Species diversity, species extinction, and ecosystem function. American Naturalist 155:696-702.

Phillips, N., Bergh, J., Oren, R., and Linder, S. 2001. Effects of nutrition and soil water availability on water use in a Norway spruce stand. Tree Physiology 21: 851-860.

Pimentel, D. and Kounang, N. 1998. Ecology of soil erosion in ecosystems. Ecosystems 1: 416-426.

Purvis, A., Agapow, P.-M., Gittleman, J.L., and Mace, G.M. 2000. Nonrandom extinction and the loss of evolutionary history. Science 288: 328-330.

Rapport, D.J., Bohm, G., Buckingham, D., Cairns, J., Costanza, R., Karr, J.R., de Kruijf, H.A.M., Levins, R., McMichael, A.J., Nielsen, N.O., and Whitford, W.G. 1999. Ecosystem health: the concept, the ISEH, and the important tasks ahead. Ecosystem Health 5: 82-90.

Rastetter, E.B., Gough, L., Hartley, A.E., Herbert, D.A., Nadelhoffer, K.J., and Williams, M. 1999. A revised assessment of species redundancy and ecosystem reliability. Conservation Biology 13: 440-443.

Raup, D.M. 1994. The role of extinction in evolution. Proceedings of the National Academy of Sciences USA 91: 6758-6763.

Read, D. 1997. The ties that bind. Nature 388: 517-518.

Reed, R.A., Peet, R.K., Palmer, M.W. and White, P.S. 1993. Scale dependence of vegetation-environment correlations: a case study of a North Carolina piedmont woodland. Journal of Vegetation. Science 4: 329-340.

Rees, M., Grubb, P.J., and Kelly, D. 1996. Quantifying the impact of competition and spatial heterogeneity on the structure and dynamics of a four-species guild of winter annuals. American Naturalist 147: 1-32.

Ricklefs, R.E. 1987. Community diversity: the relative roles of local and regional processes. Science 235: 167-171.

Roughgarden, J. 1989. The structure and assembly of communities. In: Roughgarden, J., May, R.M., and Levin, S.A. (eds), Perspectives in ecological theory. Princeton University Press, Princeton, NJ, pp. 203-226.

Schimda, A. and Ellner, S. 1984. Coexistence of plant species with similar niches. Vegetatio 58: 29-55.

Schlapfer, F. and Schmid, B. 1999. Ecosystem effects of biodiversity: a classification of hypotheses and exploration of empirical results. Ecological Applications 9: 893-912.

Schlapfer, F., Schmid, B. and Seidl, I. 1999. Expert estimates about effects of biodiversity on ecosystem processes and services. Oikos 84: 346-352.

Schlesinger, W.H. 1997. Biogeochemistry: an analysis of global change. Second edition. Academic Press, New York, NY.

Schmid, B., Hector, A., Huston, M., Inchausti, P., Nijs, I., Leadley, P., and Tilman, D. 2002. The design and analysis of biodiversity experiments. In press.

Schmidt, I.K., Michelsen, A., and Jonasson, S. 1997. Effects of labile soil carbon on nutrient partitioning between an arctic graminoid and microbes. Oecologia 112: 557-565.

Schoener, T.W. 1982. The controversy over interspecific competition. American Scientist 70: 586-595.

Schoener, T.W. 1989. The ecological niche. In: Cherrett, J.M. (Ed.), Ecological concepts: the contribution of ecology to an understanding of the natural world. Blackwell Scientific, Oxford, U.K., pp. 79-114.

Schwartz, M.W., Brigham, C.A., Hoeksema, J.D., Lyons, K.G., Mills, M.H., and van Mantgem, P.J. 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. Oecologia 122: 297-305.

Shelford, V.E. 1913. Animal communities in temperate America. University of Chicago Press, Chicago, IL.

Smith, T. and Huston, M. 1989. A theory of the spatial and temporal dynamics of plant communities. Vegetatio 83: 49-69.

Smith, T.M., Shugart, H.H., Woodward, F.I. (eds). 1997. Plant functional types: their relevance to ecosystem properties and global change. Cambridge University Press, Cambridge, U.K.

Snedecor, G.W. and Cochran, W.G. 1967. Statistical methods. Iowa State University Press, Ames, IA.

Spaekova, I. and Leps, J. 2001. Procedure for separating the selection effect from other effects in diversity-productivity relationship. Ecology Letters 4: 585-594.

Stauffer, R.C. (Ed.) 1975. Charles Darwin's Natural Selection: Being the Second Part of His Big Species Book Written from 1856 to 1858. Cambridge University Press, London, U.K.

Stohlgren, T.J., Binkley, D., Chong, G.W., Kalkhan, M.A., Schell, L.D., Bull, K.A., Otsuki, Y., Newman, G., Bashkin, M., and Son, Y. 1999. Exotic plant species invade hotspots of native plant diversity. Ecological Monographs 69: 25-46.

Swift, M.J. and Anderson, J.M. 1993. Biodiversity and ecosystem function in agricultural systems. In: Schulze, E.-D. and Mooney, H.A. (eds), Biodiversity and ecosystem function. Springer-Verlag, New York, NY, pp. 15-42.

Symstad, A.J., Tilman, D., Willson, J. and Knops, J.M.H. 1998. Species loss and ecosystem functioning: effects of species identity and community composition. Oikos 81: 389-397.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, NJ.

Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, NJ.

Tilman, D. 1996. Biodiversity: population versus ecosystem stability. Ecology 77: 350-363.

Tilman, D. 1997. Distinguishing between the effects of species diversity and species composition. Oikos 80: 185.

Tilman, D. 1999a. The ecological consequences of changes in biodiversity: a search for general principles. Ecology 80:1455-1474.

Tilman, D. 1999b. Diversity and production in European grasslands. Science 286: 1099-1100.

Tilman, D. and Downing, J.A. 1994. Biodiversity and stability in grasslands. Nature 367: 363-365.

Tilman, D. and Lehman, C.L. 1997. Habitat destructions and species extinctions. In: Tilman, D. and Kareiva, P. (eds), Spatial ecology: the role of space in population dynamics and interspecific interactions. Princeton University Press, Princeton, NJ, pp. 233-249.

Tilman, D. and Lehman, C.L. 2002. Biodiversity, composition, and ecosystem processes: theory and concepts. In: Kinzig, A.P., Pacala, S.W., and Tilman, D. (eds), The functional consequences of biodiversity. Princeton University Press, Princeton, NJ, pp. 9-41.

Tilman, D., Wedin, D., and Knops, J. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature 379:718-720.

Tilman, D., Lehman, C.L., and Thomson, K.T. 1997a. Plant diversity and ecosystem productivity: theoretical considerations. Proceedings of the National Academy of Sciences USA 94: 1857-1861.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. and Seimann, E. 1997b. The influence of functional diversity and composition on ecosystem processes. Science 277: 1300-1302.

Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T., and Lehman, C. 2001. Diversity and productivity in a long-term grassland experiment. Science 294: 843-845.

Trenbath, B.R. 1974. Biomass productivity of mixtures. Advances in Agronomy 26: 177-210.

Trenbath, B.R. 1976. Plant interactions in mixed crop communities. In: Papendick, R.I., Sanchez, P.A. and Triplett, G.B. (eds), Multiple cropping. American Society of Agronomy, Madison, WI, pp. 129-169.

Trenbath, B.R. 1978. Models and the interpretation of mixture experiments. In: Wilson, J.R. (Ed.), Plant relations in pastures. CSIRO, Australia, pp. 145-162.

Turner, R.M., Alcorn, S.M., Olin, G. and Booth, J.A. 1966. The influence of shade, soil, and water on saguaro seedling establishment. Botanical Gazette 127: 95-102.

van der Heijden, M.G.A., Klironomos, J.N., Ursic, M., Moutoglis, P., Streitwolf-Engel, R., Boller, T., Wiemken, A. and Sanders, I.R. 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature 396: 69-72.

van der Maarel, E. and Sykes, M.T. 1993. Small-scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. Journal of Vegetation Science 4: 179-188.

Vandermeer, J.H. 1970. The community matrix and the number of species in a community. American Naturalist 104: 73-83.

Vandermeer, J.H. 1972. Niche theory. Annual Review of Ecology and Systematics 3: 107-132.

Vandermeer, J.H. 1980. Indirect mutualism: variations on a theme by Stephen Levine. American Naturalist 116: 441-448.

Vandermeer, J.H. 1989. The ecology of intercropping. Cambridge University Press, Cambridge, U.K.

Vandermeer, J.H. and Boucher, D. 1978. The varieties of mutualistic interactions in population model. Theoretical Biology 74: 549-558.

Vandermeer, J., van Noordwijk, M., Anderson, J., Ong, C. and Perfecto, I. 1998. Global change and multi-species agroecosystems: concepts and issues. Agriculture Ecosystems & Environment 67: 1-22.

Vitousek, P.M. and Hooper, D.U. 1993. Biological diversity and terrestrial ecosystem biogeochemistry. In: Schulze, E.-D. and Mooney, H.A. (eds), Biodiversity and ecosystem function. Springer-Verlag, New York, NY, pp. 3-14.

Vitousek, P.M., Aber, J.D., Howarth, R.H., Likens, G.E., Matson, P.A., Shindler, D.W., Schlesinger, W.H. and Tilman, G.D. 1997. Human alteration of the global nitrogen cycle: sources and consequences. Ecological Applications 7: 737-750.

Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G., Gough, L., Dodson, S.I., Juday, G.P. and Parmenter, R. 1999. The relationship between productivity and species richness. Annual Review of Ecology and Systematics 30: 257-300.

Walker, B., Kinzig, A. and Langridge, J. 1999. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. Ecosystems 2: 95-113.

Walker, B.H. 1992. Biodiversity and ecological redundancy. Conservation Biology 6: 18-23.

Walker, T.W., Orchiston, H.D., and Adams, A.R.F. 1954. The nitrogen economy of grass legume associations. Journal of the British Grassland Society 9: 249.

Wardle, D.A. 1998. A more reliable design for biodiversity study? Nature 394:30.

Wardle, D.A. 1999. Is "sampling effect" a problem for experiments investigating biodiversity-ecosystem function relationships? Oikos 87: 403-407.

Wardle, D.A., Huston, M.A, Grime, J.P., Berendse, F., Garnier, E., Lauenroth, W.K., Setala, H., and Wilson, S.D. 2000. Biodiversity and ecosystem function: an Issue in Ecology. Bulletin of the Ecological Society of America 81: 235-239.

Watkinson, A.R. 1984. Yield-density relationships: the influence of resource availability on growth and self-thinning in populations of *Vulpia fasciculata*. Annals of Botany 53: 469-482.

Watt, A.S. 1947. Pattern and process in the plant community. Journal of Ecology 35: 1-22.

Welden, C.W. and Slauson, W.L. 1986. The intensity of competition versus its importance: an overlooked distinction and some implications. Quarterly Review of Biology 61: 23-44.

Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs 26: 1-80.

Whittaker, R.H., Levin, S.A. and Root, R.B. 1973. Niche, habitat, and ecotope. American Naturalist 107: 321-338.

Willey, R.W. 1990. Resource use in intercropping systems. Agricultural Water Management 17: 215-231.

Wilsey, B.J. and Potvin, C. 1999. Biodiversity and ecosystem functioning: importance of species evenness in an old field. Ecology 81: 887-892.

Wilson, J.B. 1999. Assembly rules in plant communities. In: Weiher, E. and Keddy, P. (eds), Ecological assembly rules. Cambridge University Press, Cambridge, U.K., pp. 130-164.

Wuenscher, J.E. 1969. Niche specification and competition modeling. Journal of Theoretical Biology 25: 436-443.

Yachi, S. and Loreau, M. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. Proceedings of the National Academy of Sciences USA 96: 1463-1468.

Zobel, M. 1997. The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? Trends in Ecology and Evolution 12: 266-269.